

## NEW DECAPOD CRUSTACEANS (THALASSINIDEA, GALATHEOIDEA, BRACHYURA) FROM THE MIDDLE OLIGOCENE OF PATAGONIA, ARGENTINA

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## ABSTRACT

A robust decapod fauna from middle Oligocene rocks near Bariloche, Argentina, has yielded several new forms. New genera include *Baricarcinus* and new species include *Callianopsis australis*, *Proterocarcinus corsolini*, *Trichopeltarion levis*, *Baricarcinus mariae*, and *Asthenognathus microspinus*. *Munda casadioi* (Schweitzer and Feldmann, 2000a) is also reported. This is the first notice of *Callianopsis* de Saint Laurent, 1973, in the southern hemisphere. The species of *Trichopeltarion* and *Asthenognathus* described herein are the oldest known representatives of their respective genera, and *Asthenognathus* is one of the oldest known genera within the Pinnotheridae de Haan, 1833. The fauna of the Foyel Formation is significantly different from that of the slightly younger Centinela Formation, exposed approximately 500 km to the south, suggesting that paleoecological conditions were conducive to specialization in the decapod fauna of southern South America.

KEY WORDS: Decapoda, Brachyura, Thalassinidea, Galatheoidea, Río Foyel, Patagonia, Oligocene, Argentina

## INTRODUCTION

The fossil decapod crustacean fauna known from southern South America is becoming increasingly robust as more and more studies are conducted in the region. Thus far, the work has been concentrated in basins known to have had direct connections with the Atlantic Ocean (Aguirre-Urreta, 1987; Feldmann et al., 1995, 1997; Schweitzer and Feldmann, 2000a, b, c, 2001a). These works have resulted in many new genera, species, and records for fossil decapod crustaceans.

The Río Foyel Formation crops out in the Andes Mountains just south of the resort town of Bariloche,

Argentina (Fig. 1), and its macroinvertebrate fauna has received little treatment to date. The recent activity of collectors in the region near Bariloche, Río Negro Province, Argentina, has resulted in a large collection of fossil decapods and other invertebrates. The new decapods described here provide an important comparison with previous studies because of the possible connection of the basin with both the Atlantic and the Pacific oceans. In fact, the decapods of the Río Foyel Formation, described here, display both Atlantic and Pacific affinities.

## GEOLOGIC SETTING

Trans-tensional stress occurring during the Oligocene resulted in a number of basins along the eastern margin of the Andes (Dalla Salda and Franzese, 1987; Ramos, 1999). The best known among them is the Ñirihuau Basin, located to the west of the Northern Patagonian Massif and east of an Oligocene volcanic arc formed

during a period of oblique convergence of the South American and Farallón plates (Spalletti and Dalla Salda, 1996). The Ñirihuau basin is an elongate (200 km) and narrow (20 to 45 km) depression bounded by strike-slip faults. The sedimentary infilling was controlled by contemporaneous tectonic and magmatic activity (Cazau,

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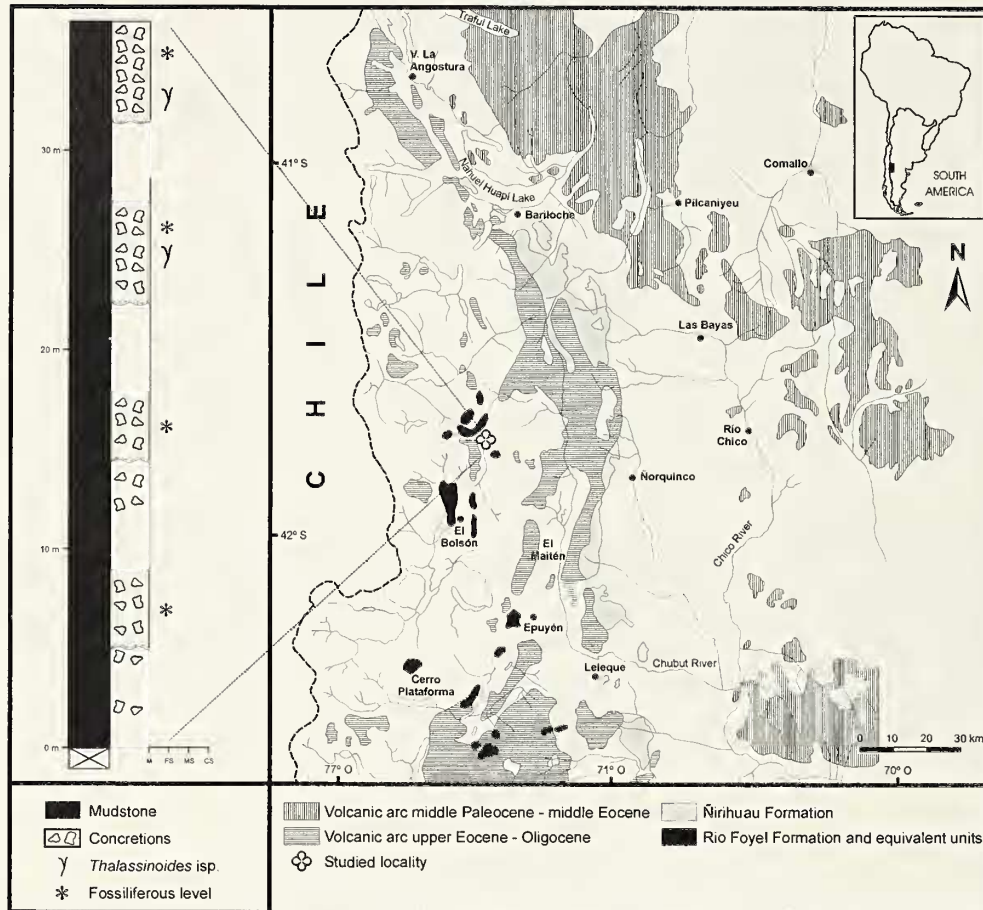


Fig. 1.—Geologic map and stratigraphic section showing the Río Foyel Formation and the position of the locality from which decapods were collected. Map modified from Spalletti and Matheos (1987).

1980; Spalletti, 1983; Franchi et al., 1984). This sedimentary infilling reaches 2,000 to 2,500 m in thickness and includes two stratigraphic units, the Ñirihuau Formation at the base and the overlying Collón Cura Formation (González Bonorino and González Bonorino, 1978; Spalletti, 1981; Cazau et al., 1989). Although both units are predominantly continental, the former includes an Oligocene event of marine sedimentation exposed along the southern coast of Lake Nahuel Huapi.

A smaller contemporaneous basin developed to the southwest, located between the Oligocene volcanic arc and the positive structural elements placed further West and which was a remnant of the Jurassic and Cretaceous volcanic arcs (Spalletti and Matheos, 1987). The sedimentary infilling of this basin includes shallow marginal lake deposits of the Ñirihuau Formation overlying marine rocks referred to the probably equivalent Río Foyel, Las Minas and Rincón de Chollila formations (Diez and Zubia, 1981). The area covered by this basin, as well as its relation to the Ñirihuau Basin, have not been determined with any degree of certainty. The textural and compositional characteristics of the infilling suggest little transport

and quick burial of the sediments in a subsiding basin associated with an undissected magmatic arc (Spalletti and Matheos, 1987). These features suggest that the Oligocene–Miocene rocks deposited to the west of the Ñirihuau Basin represent the infilling of an intra-arc basin.

The decapod crustaceans studied in this paper were collected from rocks referred to the Río Foyel Formation. These rocks are exposed along the left bank of the Foyel River (S 41° 43.589'; W 71° 27.480'), in Río Negro Province (Fig. 1). All of the decapods described herein were collected from these outcrops.

The stratigraphic section considered herein measures 36 m thick, although González Bonorino (1944) estimated that it may reach more than 150 m thick (Fig. 1). The section includes alternate beds of massive shale and concretions with irregular contact surfaces. The shales are up to 5.5 m thick and contain isolated subspherical concretions of different sizes. In some beds they are finely laminated, although the original stratification is probably diagenetically erased. The concretionary beds are up to 5 m thick and yield abundant concretions of different shapes (spherical, ovate and tubular) and sizes (0.5–20 cm



diameter). The concretions contain, in addition to the decapods studied, the coral *Flabellum* sp.; the brachiopod *Terebratella* sp.; the pelecypods *Panopea nucleus* (Ihering), *Dosinia* sp., *Neilo* sp., *Nucula* sp., *Atrina* sp., *Brachidontes* sp., *Zygochlamys* sp., and *Cucullaea* sp.; the gastropods *Turritella* sp. and *Fusinus* sp.; and the echinoderm *Schizaster?* sp., as well as vertebrate remains. Gallery tubes referred to *Thalassinoides* are also present in these beds.

The depositional paleoenvironment of this unit is controversial. Ramos (1982) and Spalletti (1983) stated that it was deposited in an open marine environment. On the other hand, Bertels (1994b) suggested the existence of unstable environmental conditions, which were fluctuating and restricted, with two events of an increase in water depth at the base and top of the sequence separated by deposits generated in very low energy marginal marine environments. Barreda et al. (2003) inferred a restricted littoral marine environment, with temperate to warm, nutrient-rich water of less than normal salinity. The lithology and the presence of concretions suggest an environment of low energy and low sedimentation rate. Fossils within the concretions exhibit fine details of the original structure, suggesting that the concretions may have formed immediately after deposition by primary precipitation by means of diagenetic reactions between sediment that was rich in organic matter and the interstitial water.

The age of the Río Foyel Formation has been the subject of diverse opinions. Bertels (1980, 1993, 1994a, b) assigned it an early middle Oligocene age based upon foraminiferans. Chiesa and Camacho (2001) stated an Eocene age, while Barreda et al. (2003) suggested it was late Oligocene–early Miocene. Pöthe de Baldis (1984) described the pollen content of this unit and recognized

two assemblages. The first one contains *Notofagidites* and low percentages of *Podocarpites*. The second assemblage yielded a low percentage of *Notofagidites*, a high frequency of trilete spores, and a significant percentage of saccate gymnosperms in which the outstanding element is *Phyllocladites mawsonii*. This would suggest an age closer to the early middle Oligocene age proposed by Bertels (1994a), as there are no modern herbaceous and arbustive elements. According to Guerstein et al. (in press), these elements are present in the Centinela Formation, indicating a modernization of the flora beginning near the Oligocene–Miocene boundary.

Ramos (1982) related the marine deposits of the Río Foyel Formation to a Pacific transgression. However, analysis of the molluscan fauna from Río Foyel, Cerro Plataforma and the valley of Epuyén support closer relationships with the Oligocene–Miocene sequence exposed along the Atlantic coast of Patagonia (Feruglio, 1949; Griffin et al., 2002). Likewise, Bertels (1980) stated that the foraminiferan assemblage from the Río Foyel Formation is the same one, albeit impoverished, found in sediments of the Atlantic Austral basin during the Oligocene–Miocene time. Thus, the paleontological evidence suggests that during Oligocene–Miocene, this basin had a strong connection with the Atlantic Ocean and perhaps a more restricted connection with the Pacific Ocean.

#### REPOSITORIES FOR TYPE AND STUDIED MATERIAL

CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.

GHUNLPam: Departamento de Ciencias Naturales, Geological Museum, Universidad Nacional de La Pampa, Santa Rosa, La Pampa, Argentina.

MSNM: Museo Civico di Storia Naturale di Milano, Milano, Italy.

#### SYSTEMATIC PALEONTOLOGY

- Infraorder Anomura MacLeay, 1838
- Superfamily Galatheoidea Samouelle, 1819
- Family Galatheididae Samouelle, 1819
- Subfamily Galatheinae Samouelle, 1819
- Genus *Munida* Leach, 1820

*Austromunida* Schweitzer and Feldmann, 2000a, p. 151, fig. 3, 4.

*Type Species*.—*Pagurus rugosus* Fabricius, 1775.

*Discussion*.—Schweitzer and Feldmann (2000a) described the new genus *Austromunida* with *A. casadioi* Schweitzer and Feldmann, 2000a, based upon three more or less complete specimens (holotype GHUNLPam 16832; paratypes GHUNLPam 16833, 16834) from the middle Eocene Centinela Formation on Estancia 25 de Mayo, Calafate, Santa Cruz (Argentina), now considered to be late Oligocene–early Miocene. Even though the authors pointed out a superficial similarity with *Munida* Leach, 1820, they justified the institution of the new genus on morphological characters not present in other

known fossil galatheids, such as the narrow, needle-like rostrum; and numerous lateral spines. However, the recent discovery of a rich sample of galatheids from Bariloche has called into question the systematic validity of *Austromunida* Schweitzer and Feldmann, 2000a. Garassino and De Angeli (2003) have synonymized *Austromunida* with *Munida*; justifications therein will not be repeated here.

*Munida casadioi* (Schweitzer and Feldmann, 2000a)  
(Fig. 2, 3)

*Diagnosis*.—Carapace subrectangular, longer than wide; central rostral spine long, needle-like; supraocular spines short, needle-like; lateral margin slightly convex, with one strong antero-lateral spine; one strong hepatic spine; three strong epibranchial spines; two strong mesobranchial spines; one strong posterior branchial spine; cervical and branchiocardiac grooves deep;



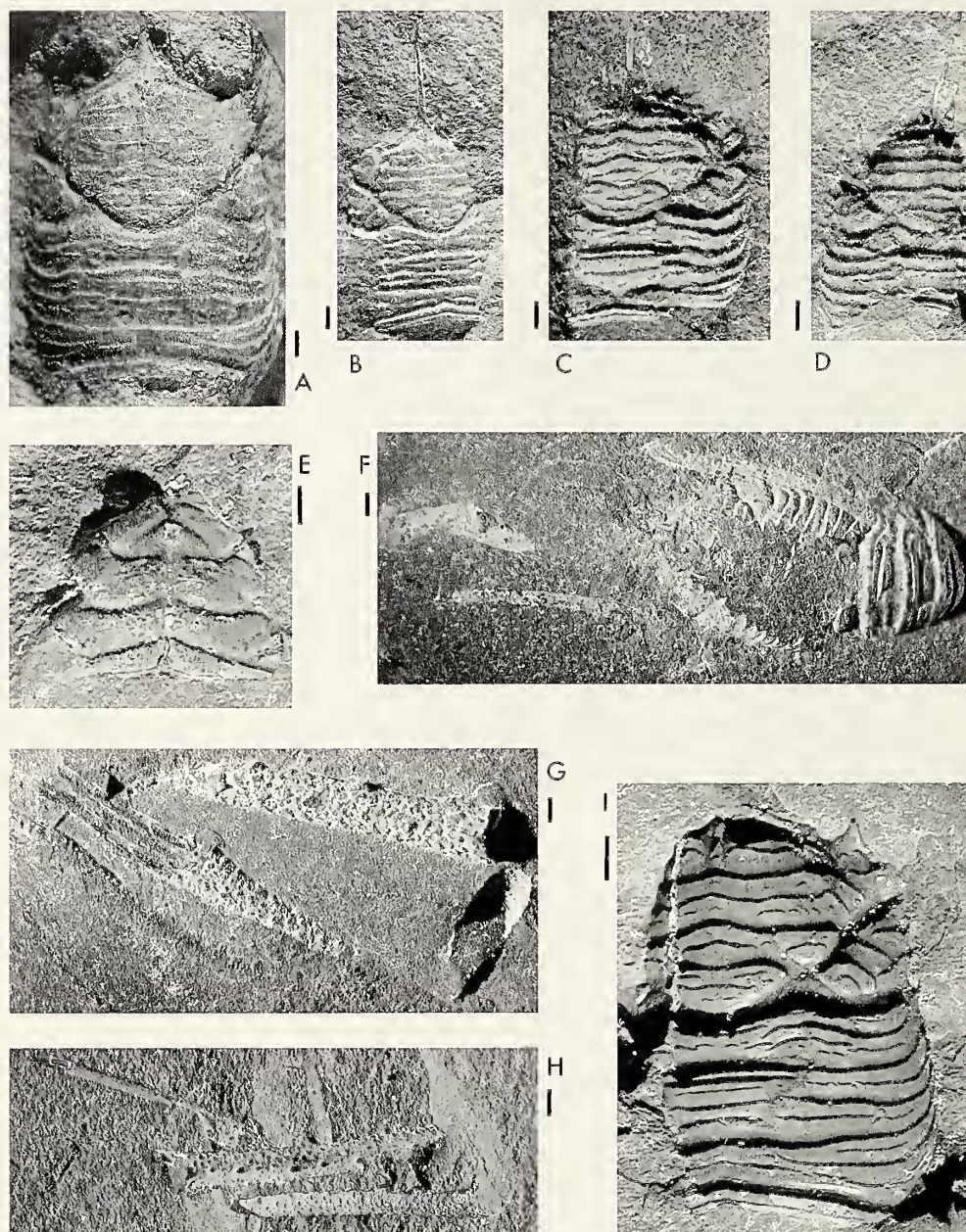


Fig. 2.—*Munida casadioti* (Schweitzer and Feldmann, 2000a). A. MSNM i26085, complete carapace with long central rostral spine, needle-like and two well-developed supraocular spines, needle-like; B. MSNM i25745, complete carapace with long central rostral spine, needle-like; C. MSNM i26087, complete carapace with long central rostral spine, needle-like and one well-developed supraocular spine, needle-like; D. MSNM i25700, complete carapace with long central rostral spine, needle-like and one well-developed supraocular spine, needle-like; E. MSNM i25799, thoracic sternites subtriangular, with arcuate striae; F. MSNM i26073, complete specimen with well-preserved abdominal somites; G. MSNM i25735, pereopods 1; H. MSNM i26088, pereopods 1; I. MSNM i25750, incomplete carapace with well-developed antero-lateral spine. Scale bars equal to 1 mm.

carapace ornamented by continuous striae and four pairs of epigastric spines, linearly arranged transversely; subtriangular thoracic sternites; pereopod 1 very elongate; abdominal somite 2 with six small spines; abdominal somite 3 with four small spines on dorsal surface.

*Material Examined.*—We ascribe to this species 164 specimens from the Bariloche area, so divided: 134 fragmentary and complete carapaces, MSNM i23031 a–b, i25627, i25629, i25630–i25649, i25651–i25658,

i25660, i25661, i25663, i25665–i25693, i25695–i25715, i25736–i25740, i25742–i25756, i25894, i26065–i26067, i26069–i26077, i26079–i26087, i26089–i26091, and GHUNLPam 25.034–25.038; 7 specimens composed of abdominal somites (MSNM i23027, i25662, i25664, i25799, i26078, i26088); 23 specimens composed of thoracic appendages (MSNM i23019, i23020, i25716–i25720, i25722–i25735, i25741, i25880, i25881, i26088).

*Measurements.*—Maximum length of the carapace ranges between 0.7 and 1.5 cm.



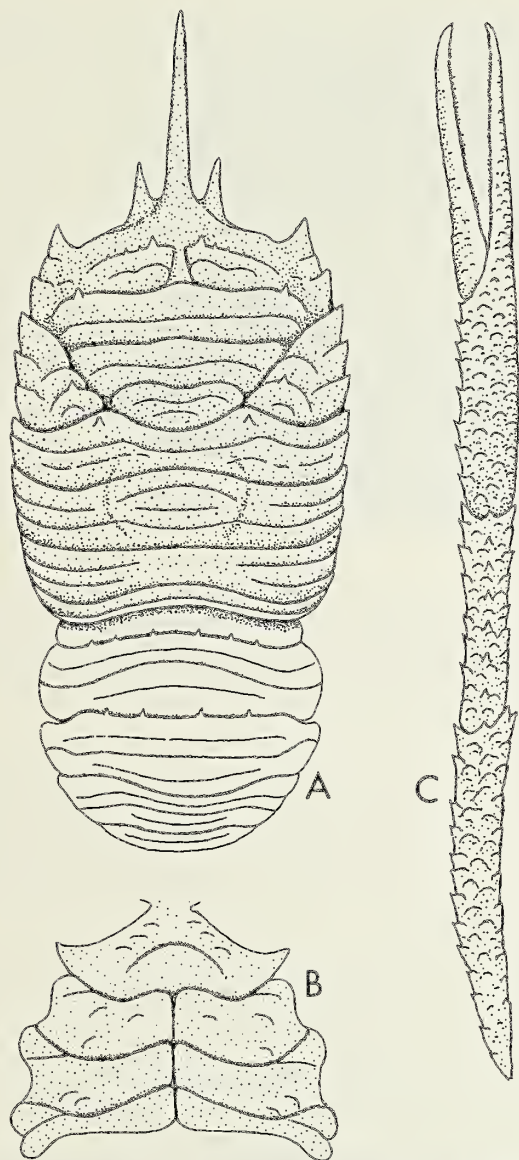


Fig. 3.—*Munida casadioi* (Schweitzer and Feldmann, 2000a). A. Reconstruction of carapace and abdomen; B. Subtriangular thoracic sternites with arcuate striae; C. Pereiopod 1.

**Description.**—Carapace, excluding rostrum, slightly longer than wide, subrectangular in dorsal view, slightly convex in transverse section and flattened in longitudinal section, with regions crossed by thin, transverse, serrated striae. Frontal margin slightly oblique. Central rostral spine long, needle-like. Orbits with concave upper orbital margin and with weak supraocular relief. Supraocular spines short, slightly convergent and directed upwards. Lateral margins of carapace long, weakly convex, with seven strong spines directed forward: one spine located in anterior anterolateral angle, one spine on hepatic margin, three on epibranchial margin, two on mesobranchial margin. Cervical and branchiocardiac grooves well developed, deep. Four pairs of epigastric spines linearly arranged transversely, median pair stronger than others. Anterior mesogastric process marked by weak groove. Small hepatic regions with small spine. Epibranchial regions marked by cervical and branchiocardiac grooves, subtriangular, with three short, sinuous striae and with one spine. Posterior regions marked by three main continuous transverse striae and more or less discontinuous minor striae.

Mesobranchial spine close to branchiocardiac groove. Cardiac region bounded on margins by weak depression. Thoracic sternites subtriangular, with arcuate striae. Second to fourth abdominal somites with four transverse striae. Abdominal somite 2 with six small submedian spines on anterior ridge. Abdominal somite 3 with four small submedian spines on anterior ridge. Pereiopod 1 chelate, very elongate. Subcylindrical merus, carpus and propodus with spines and with small, sinuous striae. Occlusal margins of dactylus and fixed finger finely serrulate.

**Discussion.**—Schweitzer and Feldmann (2000a) pointed out the main characters of *Munida*: carapace rectangular or ovoid, longer than wide; rostral spine flanked by one pair of supraorbital spines; two or three anterolateral spines; several small, lateral spines posterior to intersection of cervical groove with lateral margin; deep, arcuate cervical groove; transverse carapace ridges that range from simple and parallel to complex and bifurcating; and a linear array of gastric spines paralleling frontal margin of carapace. The main characters of *Munida* can be found in the study specimens.

This genus is known in the fossil record from four species, distributed from the Danian (Lower Paleocene) to Miocene: *Munida primaeva* (Segeber, 1900) from the Danian of Denmark; *M. quadrolonga* Schweitzer and Feldmann, 2000a, from the Eocene of Washington, USA; *M. konara* Schweitzer and Feldmann, 2000a, from the Oligocene–Miocene of Alaska; and the middle Oligocene to Miocene *M. casadioi*. Two indeterminate species are also known from the Miocene of Japan (Segeber, 1900; Takeda et al., 1986; Collins and Jakobsen, 1994; Jakobsen and Collins, 1997; Schweitzer and Feldmann, 2000a; Kato, 2001).

Collins and Jakobsen (1994, tab. 10, fig. 2) and Jakobsen and Collins (1997, tab. 2, fig. 8) reported the presence of *Munida primaeva* in the decapod fauna from the Danian of Denmark, without giving its morphological description. The poor state of preservation of the lectotype of this species, lacking the rostral spine and the supraorbital and anterolateral spines, makes comparison with *M. casadioi* (Schweitzer and Feldmann, 2000a) difficult. However, the presence of two epigastric spines, one spine on the epibranchial region, and one spine on the posterior branchial region distinguish *M. casadioi* from the Danish species.

*Munida quadrolonga* was described on two more or less complete specimens (Schweitzer and Feldmann, 2000a, p. 154, fig. 6). *Munida casadioi* differs from this species because *M. casadioi* has only one anterolateral spine, only two epigastric spines, one spine in the hepatic region and one spine on hepatic margin, three spines along the epibranchial margin and two on the mesobranchial margin. *Munida konara* was described based upon five very incomplete specimens (Schweitzer and Feldmann, 2000a, p. 156, fig. 7). Even though the comparison between *M. casadioi* and *M. konara* is difficult because of the poor state of preservation of the latter species, the presence of only one anterolateral spine distinguishes *M. konara* from *M. casadioi*. In addition, the carapace of *M. konara* is broader than *M. casadioi*.

Infraorder Thalassinidea Latreille, 1831  
 Superfamily Callianassoidea Dana, 1852  
 Family Ctenochelidae Manning and Felder, 1991  
 Genus *Callianopsis* de Saint Laurent, 1973

*Included Species*.—*Callianopsis anstralis* new species; *C. callamensis* (Withers, 1924); *C. goniophthalma* (Rathbun, 1902) (recent only); *C. muratai* (Nagao, 1932) (= *Callianassa elongatodigitata* Nagao, 1941; *Callianassa kusiroensis* Nagao, 1941); *C. titaensis* (Nagao, 1941); *Callianopsis* spp. Kato, 1996; ?*C. inornatus* Schweitzer and Feldmann, 2001b. Unless otherwise marked, all are exclusively fossil.

*Diagnosis*.—Carapace with dorsal oval and cardiac prominence; low rostral carina, rostral spine; sixth abdominal somite with lateral projections; uropod lacking notch or incision; major cheliped with proximal meral hook and keel; carpus of major cheliped with flange extending from lower margin. Manus of male rectangular, with large tubercles on outer surface; distal margin with spine at midheight; fixed finger with spine or prominence at midlength; movable finger usually with large nodes and keel on outer surface. Manus of female narrow, gracile, with smaller tubercles on outer surface; movable finger with small nodes and less robust keel. Minor chela smaller and more slender than major chela (after Manning and Felder, 1991; Schweitzer-Hopkins and Feldmann, 1997).

*Discussion*.—Although only one extant species of *Callianopsis* is known, there are several fossil species. The morphology of the major cheliped is remarkably consistent throughout the genus, with species being differentiated primarily by the ornament on the manus and the shape of the merus. *Callianopsis* is notable in displaying very distinct sexual dimorphism, recognizable in fossil and extant species (Schweitzer-Hopkins and Feldmann, 1997).

The new material exhibits nearly all of the generic level diagnostic features of the major chela; the carapace is unavailable for study. The only generic features that are missing in the new material concern the ornamentation on the fixed finger and the swelling along the distal margin of the manus. However, these regions of the new fossil material are crushed or broken; thus, it is not possible to observe them. The manus of the minor chela is somewhat more stout than in other species of the genus, but it is still much smaller than the major chela. Thus, the new material is confidently referred to *Callianopsis*.

The discovery of a species of *Callianopsis* in the southern hemisphere represents a major range extension. Other fossil species of *Callianopsis* are known only from the North Pacific realm, while the sole extant species ranges from coastal Alaska to Baja California. The oldest known species is possibly *Callianopsis? inornatus* from Eocene rocks of the Olympic Peninsula, Washington (Schweitzer and Feldmann, 2001b), and the oldest species known with certainty are those named by Nagao (1941) from the Eocene of Japan. The extension of the

geographic range to the middle Oligocene of Patagonia suggests that the genus had an amphitropical distribution by the late Oligocene. The genus appears to have originated in the North Pacific Ocean during the Eocene and subsequently dispersed to the high southern latitudes, perhaps by moving into deeper, colder water to cross the equatorial region. The extant species, *C. goniophthalma*, is known from deep-water localities and is restricted to west coastal North America, which is bathed by cool-water currents from the North (Schweitzer-Hopkins and Feldmann, 1997). It appears to be quite possible that the distribution of the genus is controlled by temperature factors as well as depth preferences, because all fossil species are known from moderate to high latitudes and the extant species is known from deep, cool water areas.

*Callianopsis australis*, new species  
 (Fig. 4)

*Types*.—Holotype, GHUNLPam 25.000 and 2 paratypes, GHUNLPam 25.001 and 25.002; paratypes MSNM i25608, i25613–i25616, i25626; CM 52515, cast of MSNM i25626; CM 52516, cast of MSNM i25608; CM 52522, cast of GHUNLPam 25.000.

*Diagnosis*.—Merus of major cheliped stout, with very small spine on proximal lower margin; manus of major cheliped of male with large tubercles distally, distal margin with blunt spine above position of fixed finger; fixed finger of male chela curving upward, with long, blunt projection on occlusal surface; manus of minor chela stout for genus.

*Etymology*.—The trivial name is the Latin word *australis*, meaning southern, in reference to this species of the genus being the first known from the Southern Hemisphere.

*Description*.—Ischium of major cheliped longer than high, highest distally and narrowing proximally; upper margin convex distally and becoming concave proximally; distal margin sinuous, convex at upper margin at articulation with carpus, concave at lower margin; lower margin weakly concave; remainder of article unknown.

Merus of major cheliped not much longer than high, L/H about 1.6, bulbous; with blunt, longitudinal keel dividing merus longitudinally into two portions, upper portion much larger; proximal margin nearly straight; lower margin with very small spine at proximal corner, spine directed downward, remainder of margin convex; distal margin angular, facilitating articulation with carpus; upper margin markedly convex.

Carpus of major cheliped higher than long, L/H about 63 percent, proximal margin with long projection at upper corner at articulation with merus, remainder convex, merging with lower margin; lower margin bounds a flange extending downward from main portion of article; upper margin weakly convex; distal margin weakly concave.

Manus of male major cheliped longer than high, H/L averaging about 92 percent, rectangular, ornamented with large tubercles distally, moderately vaulted longitudinally especially distally, moderately vaulted transversely especially along upper margin; proximal margin with small projection at upper corner at articulation with carpus, with small notch under projection, remainder of margin nearly straight; upper margin nearly straight; lower margin proximally weakly convex, becoming concave just proximal to fixed finger; distal margin straight at upper portion, becoming sinuous with blunt spine just above position of fixed finger; inner surface smooth, weakly convex centrally.

Fixed finger curving upward, with long, blunt projection on occlusal surface, shorter and narrower than movable finger. Movable finger stout,



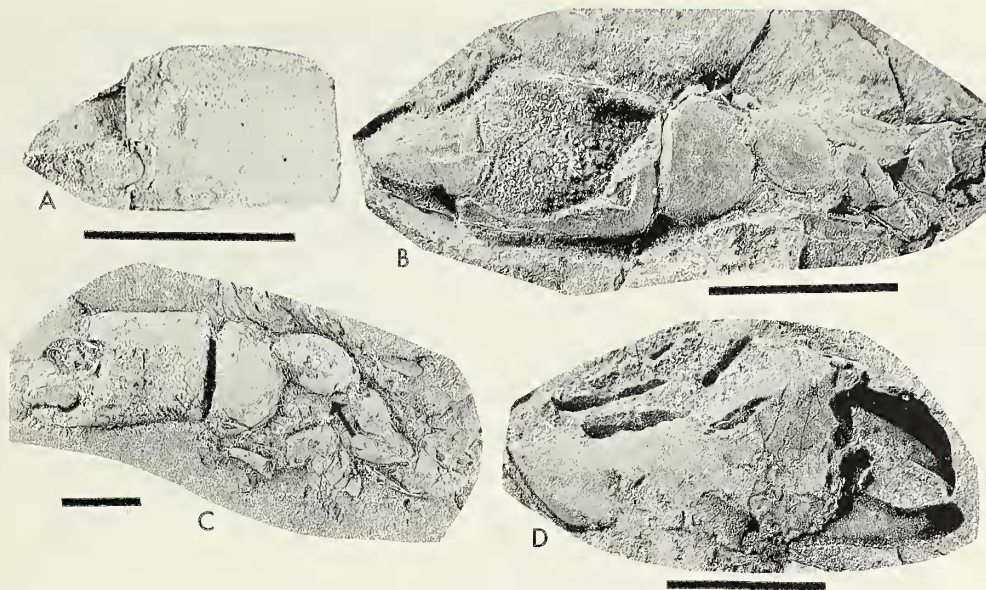


Fig. 4.—*Callianopsis australis* new species. A. Exaflex© cast of manus of major chela, paratype MSNM i25608 (counterpart), showing granular ornamentation; B. Major cheliped, paratype MSNM i25608 (part); C. Major cheliped, and portion of minor cheliped, holotype GHUNLPam 25.000, arrow indicates tiny spine on merus diagnostic for genus; D. Portion of manus and fingers of major chela, showing granular ornamentation on lower margins of manus and fixed finger, paratype MSNM i25616. Scale bars equal to 1 cm.

narrowing distally, weakly arched; with blunt tooth proximally, possibly articulating with blunt spine on distal margin, to be used for crushing.

Manus of minor chela of similar shape to major chela but much smaller.

Remainder of appendages and carapace unknown.

**Measurements.**—Measurements (in mm) taken on articles of the major cheliped of specimens of *Callianopsis australis*: GHUNLPam 25.000: maximum length of manus (L1), 15.2; maximum height of manus (H1), 13.0; length of fixed finger (L2), >6.6; length of movable finger (L3), >11.3; maximum height of carpus (H2), 13.0; maximum length of carpus (L4), 6.9; maximum length of merus (L5), 9.7; maximum height of merus (H3), 7.2; MSNM i25608: L1, 10.0; H1, 9.0; L5, 9.7; H3, 7.2; GHUNLPam 25.001: L1, 15.7; H1, 14.9; MSNM i25626: L1, 7.4; H1, 7.0; L3, 4.3; H2, 6.0; L4, 6.9; L5, 5.0; H3, 2.9.

**Discussion.**—*Callianopsis australis* is represented by one very well preserved specimen, retaining the manus, carpus, merus, and ischium, and four rather poorly preserved specimens. However, each has contributed to the description of the species. The meral hook, while tiny (Fig. 4C), is clearly exhibited on the holotype, GHUNLPam 25.000. The movable finger of GHUNLPam 25.001 exhibits a tiny portion of keel proximally, but the remainder is crushed.

*Callianopsis australis* can be differentiated from other species by its blunt projection on the fixed finger; all other species have a spine in that position. The merus is more stout in *Callianopsis australis* than in the other species of the genus, and the minor chela is more stout in *C. australis* than in other species, in which it is slender and gracile.

The specimens of *Callianopsis australis* all appear to be males because they exhibit the rectangular manus and heavy ornamentation typical of males of *Callianopsis* (Schweitzer-Hopkins and Feldmann, 1997). However, the specimens range considerably in size, and the two smaller specimens may be juveniles, which have less differentiated chelae and are thus of indeterminate gender in fossils (Schweitzer-Hopkins and Feldmann, 1997).

Infraorder Brachyura Latreille, 1802  
Section Heterotremata Guinot, 1977  
Superfamily Portunoidea Rafinesque, 1815  
Family Portunidae Rafinesque, 1815  
Subfamily Polybiinae Ortmann, 1893

Genus *Proterocarcinus* Feldmann, Casadío, Chirino-Gálvez, and Aguirre-Urreta, 1995

**Type Species.**—*Proterocarcinus lophos* Feldmann, Casadío, Chirino-Gálvez, and Aguirre, Urreta, 1995, by monotypy.

**Other Species.**—*Proterocarcinus latus* (Glaessner, 1933), as *Archaeogeryon*; *Proterocarcinus corsolini* n. sp. herein.

**Diagnosis.**—Carapace transversely ovoid to hexagonal, wider than long, 0.60–0.76 times as long as wide; front narrow, downturned, with four spines including inner-orbital spines; orbits extremely broad, rimmed, fronto-orbital width to width ratio 0.70–0.95, two orbital fissures; anterolateral margin short, with four spines including outer-orbital spines; epibranchial ridge elevated, granular, terminating at base of fourth anterolateral spine; branchial region swollen, with longitudinal ridge

parallel to long axis of cardiac region; first pereopods isochelous; propodus and dactylus of fifth pereopod paddle-like (Schweitzer and Feldmann, 2000b, p. 644).

*Discussion.*—The genus was originally described based upon specimens collected from Danian rocks of the Roca Formation in the Neuquén Basin, Río Negro Province, Argentina and subsequently was identified in the upper Oligocene–lower Miocene Centinela Formation in Santa Cruz Province. Thus, it is possible that the genus spans much of the Cenozoic.

Although identification of species referable to *Proterocarcinus* based upon the diagnostic characters is straightforward, there is the potential for confusion based upon the discovery that juvenile specimens of *Chaceon peruvianus* (d'Orbigny, 1842) bear a strong resemblance to adult *Proterocarcinus latus* (Glaessner, 1933) (Schweitzer and Feldmann, 2000b). Details of surface morphology and ornamentation are strikingly similar although the width of the fronto-orbital margin is very great in juvenile and adult *Proterocarcinus* (FOW/W = 0.84–0.91) whereas that margin is somewhat narrower in juvenile *Chaceon* Manning and Holthuis, 1989 (FOW/W = 0.80–0.82) and much narrower (FOW/W = 0.52–0.63) in adults. Additionally, the anterolateral margin of *Chaceon* bears five spines, and there are fewer than five in *Proterocarcinus*.

The problem of distinguishing between species of the two genera has been made more confusing by the addition of the generic name, *Lebucarcinus* Bahamonde and Frassinetti, 1980, that may be a synonym of *Chaceon*. Bahamonde and Frassinetti (1980) proposed this name in recognition that a species named *Cancer tyro* by Philippi (1887) was not a member of *Cancer*. Unfortunately, the holotype of *Cancer tyro* illustrated by Philippi (1887, pl. 50, fig. 3) apparently no longer exists. Bahamonde and Frassinetti (1980) noted that it had been in the collection of Francisco J. Ovalle, but they did not indicate that they had confirmed that the type was missing. Chirino-Gálvez (1993), citing Porter (1910), concluded that the specimen was probably lost in the earthquake and fire of 1906 in Chile. The type is not in the collections of the Museo Nacional de Historia Natural, Santiago, where many of Philippi's types are deposited. As a result, Bahamonde and Frassinetti (1980, p. 276) designated SGO.PI.3422 in the Museo Nacional de Historia Natural, Santiago, as the neotype of *Cancer tyro*. The neotype bears no resemblance to the illustration of the type specimen of *Cancer tyro* nor does it fit the type description. Furthermore, the neotype was collected at Punta de Fraile, some 65 km north from the type locality at Lebu. Thus, the validity of the type designation, and therefore the validity of the name *Lebucarcinus* is called into question (International Code of Zoological Nomenclature, 1999, Article 75).

The original description of *Cancer tyro* is: "Cephalothorax subhexagonal, wider than long, moderately convex above, granulo-squamose on protuberances, depressed

parts very smooth; front margin entirely semi-orbicular, lateral margin entirely straight, posterior margin somewhat arcuate, extended, half the breadth of cephalothorax flattened, front weakly downturned, tridentate, teeth very short, truncated." (Philippi, 1887, p. 214, translated from Latin by the authors) The Spanish elaboration on the description is: "A wide transverse depression, almost horizontal, extends behind the orbits from one side to the other; the margin of the carapace, which corresponds to this depression, is broken. The genital and cardiac regions are almost exactly the same size and same form and terminate on each side in a point; the former is extended toward front in a well-marked beak. The form of these regions is almost as that observed in the genus *Pseudocarcinus* [error pro *Pseudocarcinus*] [H.] Milne Edwards. Both regions are granulose, another similarity is the three lateral protuberances which lie on either side. The extremity of the left hand is preserved, the fingers are very slender and the index is very flattened and armed with very fine, closely spaced teeth." (Philippi, 1887, p. 214, translated from Spanish by the authors)

Examination of the single illustration of the specimen referred to *Cancer tyro* by Philippi (1887) shows that the specimen had a length/width ratio of 0.86, a frontal width/width ratio of 0.23, a fronto-orbital width/width ratio of 0.46, and a posterior width/width ratio of 0.4. These values fall within or are close to the ratios taken from adult specimens of *Chaceon peruvianus* (Schweitzer and Feldmann, 2000b). Furthermore, the anterolateral margin, although broken, seems to be quite irregular as though it bore several spines.

By contrast, the description of *Cancer tyro* given by Bahamonde and Frassinetti (1980), based upon the neotype and one additional specimen referred to the species, SGO.PI.3443, is: "Cephalothorax subpentagonal, densely granulated, slightly convex, rather flattened, with anterolateral margin containing two large, subequal spines located in its posterior half. Base of anterior spine a little wider than base of posterior spine, both have smooth borders. Posterolateral margins nearly straight, very gently curved.

"Orbits are rather wide, well defined, with a thick raised margin, with external corner not dentiform, smooth without spines or prominent granules. Front narrow, slightly inclined downwards, smoothly trilobed; the metagastric and cardiac lobes identifiable. Posterior margin of the carapace smooth with well pronounced border, finely granulated.

"Chelipeds well developed, large, but not strong; right a little more developed than left, with the propodus a bit shorter. Propodus slightly scaly, provided externally with three carinae, one large, another medium and very noticeable, and one small; the uppermost parts are the most scaly. Fingers are thin, with fine closely spaced teeth, black in color.

"The ambulatory legs are finely and uniformly granulated, with the merus smooth, relatively wide and



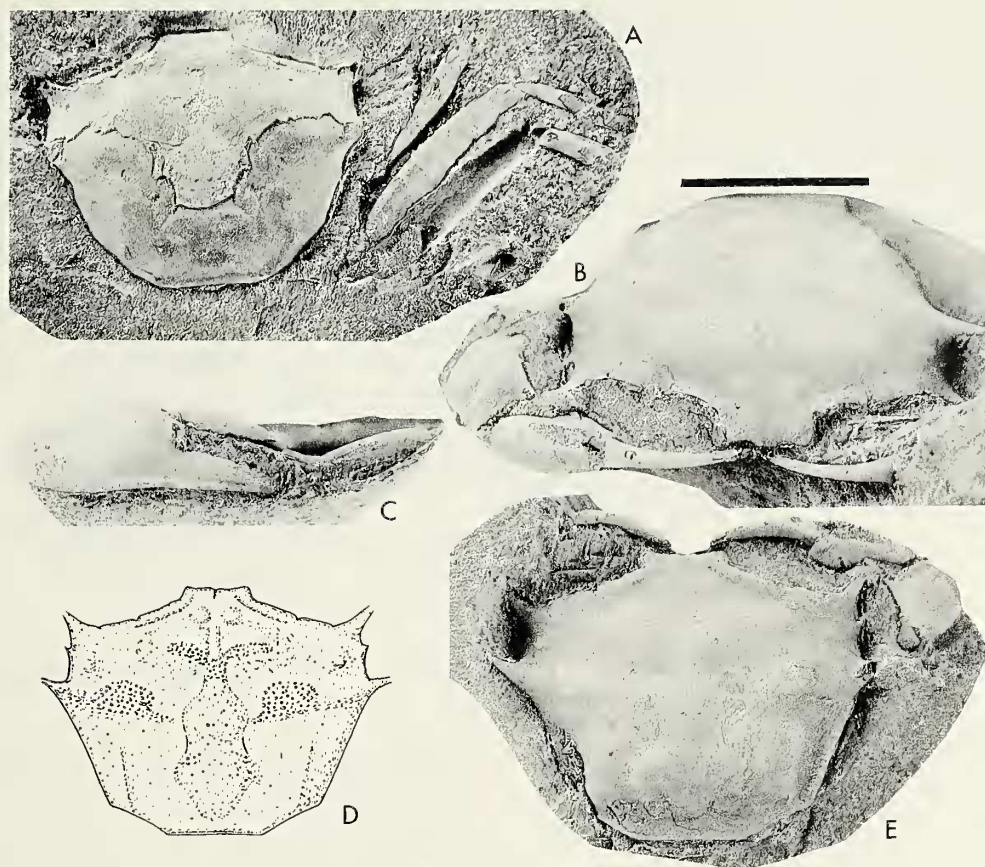


Fig. 5.—*Proterocarcinus corsolini* new species. A. Dorsal carapace and appendages, paratype MSNM i25803a; B. Oblique anterior view of dorsal carapace, showing orbits and rostrum, holotype GHUNLPam 25.010; C. Cheliped of holotype, GHUNLPam 25.010; D. Composite line drawing of dorsal carapace; E. Dorsal carapace of holotype, GHUNLPam 25.010. Scale bar equal to 1 cm.

flattened. Only the first four pairs of legs can be seen while the fifth one is not visible. No significant remains of the abdomen have been found.

"The stridulating apparatus is clearly defined." (Bahamonde and Frassinetti, 1980, p. 276, translated from Spanish by Luis Chirino-Gálvez)

The dimensions taken from the neotype of *Cancer tyro*, SGO.PI.3422, are almost precisely those of *Proterocarcinus latus* (Schweitzer and Feldmann, 2000b); frontal width/width = 0.17; fronto-orbital width/width = 0.87; posterior width/width = 0.30, and length/width = 0.76. The orbital margin is very long, straight, and sloping posteriorly. The anterolateral margin bears two large spines; if other, intermediate spines exist, they are not visible on the low resolution photographs. These are all characteristics of *P. latus*.

Accordingly, we therefore conclude that the neotype designated by Bahamonde and Frassinetti (1980) for *Cancer tyro* should be rejected on the grounds that they published the neotype and the new generic name solely for that purpose (ICZN, 1999, Article 75.2), they did not adequately document the loss of the holotype (ICZN, 1999, Article 75.3.4), the description and illustrations of the neotype do not conform to the sense of the original

designation both in terms of the description and the illustration by Philippi (1887) (ICZN, 1999, Article 75.3.5), and the neotype was not collected near the type locality (ICZN, 1999, 75.3.6). Further, we conclude that the original description of *Cancer tyro* (Philippi, 1887) lies within the boundaries of *Chaceon*.

The specimen designated as the neotype of *Cancer tyro* and, therefore, the type species of *Lebucarcinus*, most closely conforms to the sense of *Proterocarcinus*. Thus, we place the specimens studied by Bahamonde and Frassinetti into *Proterocarcinus*. Finally, following the rules of nomenclature, the removal of the type species from *Lebucarcinus* renders the generic name a *nomen nudum*.

#### *Proterocarcinus corsolini*, new species (Fig. 5)

*Types*.—Holotype, GHUNLPam 25.005, and paratypes GHUNLPam 25.006–25.033; paratypes MSNM i23005, i23030, i25802, i25803, i25822; possibly chela GHUNLPam 25.074; paratypes CM 52505–52507; CM 52517, cast of MSNM i25803; CM 52518, cast of MSNM i25822; CM 52524, cast of GHUNLPam 25.074.

Table 1.—Measurements (in mm) taken on the dorsal carapace of specimens of *Proterocarcinus corsolini*. L = maximum carapace length; W = maximum carapace width; FW = frontal width; FOW = fronto-orbital width; PW = posterior width.

Specimen	L	W	FW	FOW	PW
GHUNLPam 25.010 Holotype	16.1	18.5	4.7	16.7	6.1
GHUNLPam 25.011	11.9	14.2	—	12.1	4.8
MSNM i125803a	16.2	19.8	4.6	17.1	7
GHUNLPam 25.012	19.8	23.8	6.4	—	8.9
CM 52505	~10.6	11.8	—	10.6	4.2
MSNM i125581	16.6	20.2	4.8	16.2	6
GHUNLPam 25.029	18.4	22.2	6.4	21.4	7.1
CM 52506	ca. 16.6	20.1	—	19.2	7.5
GHUNLPam 25.007	11.7	13.1	2.8	12	4.3
MSNM i123005	11.4	13	2.8	11.5	4.9
GHUNLPam 25.013	~27	~29.4	7.4	26.4	—

**Diagnosis.**—*Proterocarcinus* with moderately broad frontal margin bearing four broadly rounded teeth; long orbital margins that slope posterolaterally; three anterolateral teeth, the medial one of which is greatly reduced; and moderately well-defined carapace regions with distinct longitudinal ridge on metabranchial region.

**Etymology.**—The trivial name recognizes the contribution of Rodolfo Corsolini, Museo del Lago Gutiérrez "Dr. Rosendo Pascual" in Bariloche, Río Negro, Argentina, who collected much of the material described in this study and who assisted the authors in the field.

**Description.**—Moderate sized for genus. Carapace generally quadrate in outline, longer than wide; weakly arched transversely, more strongly vaulted longitudinally; regions weakly defined as elevated areas.

Front broad, 24 percent maximum width, excluding spines, more or less straight, downturned, with two blunt inner orbital projections and bilobed axial projection. Orbits very broad, well-defined orbital rim becoming obscure laterally; fronto-orbital width about 88 percent maximum width, straight, sloping posterolaterally to terminate in anterolaterally projecting anterolateral spines; two small orbital notches, one at midlength and one near base of outer orbital spine. Anterolateral margin shorter than posterolateral margin, straight, nearly parallel long axis, with three anterolaterally directed spines including outer orbital spine; medial spine small or reduced to node. Posterolateral margins straight, well defined, converging posteriorly. Posterior corners truncated as long, straight elements bounding moderately wide, straight posterior margin, about 32 percent maximum width.

Regions of carapace defined as broad, slightly swollen areas with granular surfaces separated by broad, shallow depressed areas. Frontal region extends to level of medial orbital fissures, well defined as swollen areas flanking shallow, axial sulcus. Hepatic regions weakly defined, bearing centrally located node at level of second anterolateral spine. Protogastric regions large, weakly elevated to form transverse ridge with granular surfaces, separated by long, narrow mesogastric region, broadening slightly posteriorly to level of last anterolateral spine then widening abruptly to merge with metagastric region which bears pair of small pits and is flanked by well defined arcuate grooves. Cardiac region very broad; with subtle transverse ridge, weakly depressed axially; narrowing posteriorly into indistinct intestinal region. Mesobranchial region with broad, distinct ridge extending from metabranchial region to last anterolateral spine. Metabranchial region with narrow, distinct longitudinal ridge defining steeply sloping lateral portion of metabranchial region and terminating just inside posterolateral corner.

Abdomen and venter not known.

First pereopods isochelous. Carpus nearly equidimensional when viewed from above, strongly inflated, keel defines outer margin. Keel extending transversely parallel to distal margin, with prominent spine on inner distal corner. Propodus longer than high, maximum height at distal

end of hand, keeled on upper surface; broad ridge extends from lower articulation with carpus to base of articulation with dactylus. Lower margin weakly concave, keeled to tip of fixed finger. Length of fixed finger about equal to length of hand. Dactylus smooth; upper surface curved downward toward tip; curved slightly toward posterior when viewed from above. Denticles of occlusal surfaces poorly preserved, appear to be moderately large, blunt spines with darkened tips.

**Measurements.**—Measurements, in millimeters, taken on specimens of *Proterocarcinus corsolini* are given in Table 1.

**Discussion.**—The description of *Proterocarcinus corsolini* brings to three the number of species referred to *Proterocarcinus*. As discussed above, it is probable that some Chilean specimens, previously referred to the genus *Lebucarcinus* should be assigned to *Proterocarcinus*; however, that decision must await examination of the specimens in question. In addition, Aguirre Urreta (1987) referred specimens from Península Valdés, Chubut Province, Argentina, to *Lebucarcinus tyro*. In all likelihood, this material, which is currently being restudied, is referable to *Proterocarcinus*.

*Proterocarcinus corsolini* shares generic characteristics with the two previously described species; but, it can readily be distinguished from them. Although the front is not known from the type species, *P. lophos*, the anterolateral margin exhibits four prominent spines and the dorsal surface has subdued topography and lacks clear longitudinal ridges on the metabranchial regions. By contrast, *P. corsolini* has three anterolateral spines, the medial one being reduced; the regions are more distinctly defined; and a prominent longitudinal ridge extends across the metabranchial region. *Proterocarcinus latus* exhibits a dorsal surface that is reminiscent of *P. corsolini*, but the former species has four anterolateral spines, the medial two of which are reduced; the orbital margin does not slope posterolaterally to the same extent that it does in *P. corsolini*; and the rostrum is more projected and bears more prominent teeth. The ratio of frontal width to total width is 17 percent in *P. latus* and 24 percent in *P. corsolini*.

Superfamily Cancroidea Latreille, 1802

Family Atelecyclidae Ortmann, 1893

Genus *Trichopeltarion* A. Milne Edwards, 1880

*Trichopeltarion* A. Milne Edwards, 1880:19.

*Trachycarcinus* Faxon, 1893:156.

**Type Species.**—*Trichopeltarion nobile* A. Milne Edwards, 1880, p. 20, pl. 2.

**Included Species.**—See Schweitzer and Salva (2000) and Salva and Feldmann (2001).

**Diagnosis.**—A recent diagnosis of the genus was given by Salva and Feldmann (2001) and will not be repeated here.

**Discussion.**—*Trichopeltarion* and related genera have recently been studied in depth (Schweitzer and Salva, 2000; Salva and Feldmann, 2001) so that a re-examination of the details of definition of the genus is not



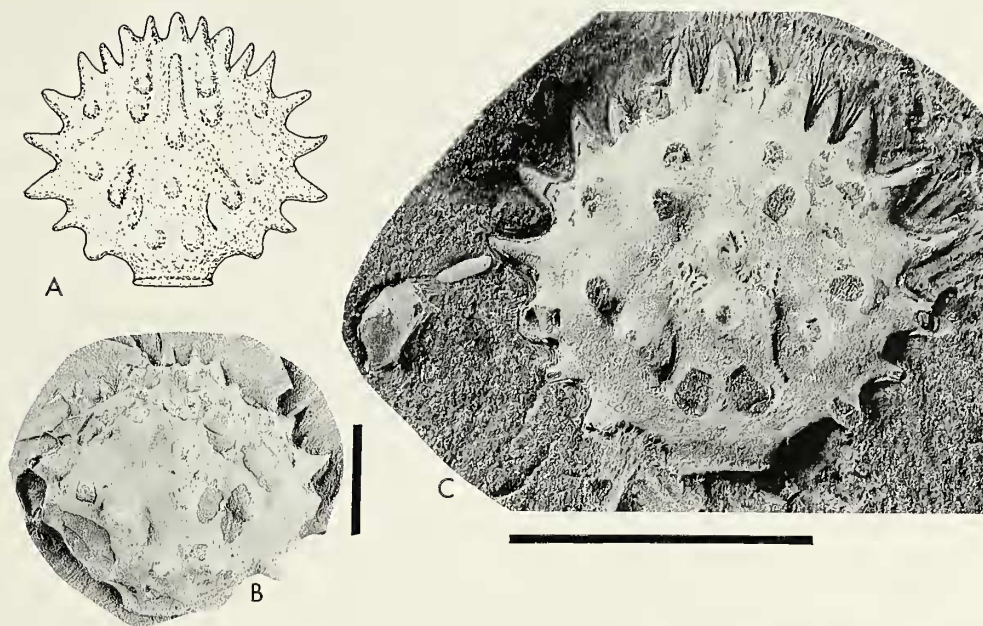


Fig. 6.—*Trichopeltarion levis* new species. A. Composite line drawing of dorsal carapace; B. Dorsal carapace, holotype GHUNLPam 25.040; C. Dorsal carapace, paratype MSNM i25533. Scale bars equal to 1 cm.

necessary herein. The specimens from the Bariloche region conform to the generic diagnosis of the carapace in all regards so that placement within the genus is certain. The carapace is nearly circular, the rostrum is not strongly produced and is trifid, the upper orbital margin bears three spines separated by deep clefts, the lateral margins exhibit simple spines, and the regions tend to be swollen, separated by broad, shallow grooves, and with discrete spines.

*Trichopeltarion* has the most robust fossil record of any member of the Atelecyclidae. The new species described here is the oldest known species of the genus. *Trichopeltarion berglundorum*, from late Oligocene to early Miocene age rocks in Washington state (Schweitzer and Feldmann, 1999), is the second oldest species of the genus. Thus, this suggests that the genus arose in the southern hemisphere with subsequent dispersal to the northern hemisphere and also westward into the western Pacific and Indian oceans (Table 3). *Levicylus* Schweitzer et al., 2002, is known from Eocene rocks of Baja California Sur, México, which marks the earliest known occurrence of the family. *Atelecyclus* Leach, 1814, has been reported from Miocene to Pleistocene occurrences in North Africa and Europe (Glaessner, 1969), but these occurrences have yet to be verified.

*Trichopeltarion levis*, new species  
(Fig. 6)

**Types.**—Holotype GHUNLPam 25.040, paratypes GHUNLPam 25.039, 25.041, 25.042; paratypes, i23026, i25524a and b, i25528a and b, i25533a and b; paratypes CM 52500–52504; CM 52514, cast of MSNM i25533; CM52523, cast of GHUNLPam 25.039.

**Diagnosis.**—Carapace ornamented only by very fine pustules; frontal, orbital, and lateral spines simple; posterolateral spines well developed; carapace regions bearing 14 prominent, simple spines.

**Etymology.**—The trivial name is from the Latin *levis*, meaning smooth, referring to the generally smooth carapace surface.

**Description.**—Carapace small for genus, circular, transversely and longitudinally vaulted; bearing simple spines on front and lateral margins and prominent, sharply-pointed spines on dorsal surface.

Front trifid, not extended significantly beyond margin, with elongated spines of equal length with rounded terminations; median spine broader than lateral ones. Orbits directed weakly anterolaterally, defined by three spines; inner orbital spine approximately equilateral; medial and outer orbital spines more slender; outer orbital spine curved anteriorly. Two anterolateral spines, slender, simple, curved slightly anteriorly. Three posterolateral spines, decreasing in length posteriorly; anteriormost stout, equilateral; medial spine narrow, elongate; posteriormost spine defined as blunt protuberance. Posterior margin sharply defined, produced posteriorly, with prominent, thickened, pustulose rim.

Regions of carapace defined by subtle, broad depressions. Mesogastric region elongate, slender anteriorly, broadening posteriorly and bearing prominent spine near posterior margin. Protogastric regions elongate, narrow, extending from outer frontal spine weakly posterolaterally; bearing two spines arrayed on either side of midline of carapace, anteriormost spine smaller than prominent, domal posterior one. Metagastric region nearly circular, with strong axial spine. Urogastric region not differentiated. Cardiac region defined laterally by deep, arcuate branchiocardiac grooves and bearing pair of prominent spines arrayed transversely. Intestinal region depressed with subtle axial swelling. Hepatic region a weak swelling with centrally located spine. Gastric regions not well differentiated, bearing two prominent spines set equidistant from posterolateral margin. Surface of carapace ornamented by extremely fine pustules.

Remainder of organism not preserved.

**Measurements.**—Measurements, in mm, taken on the dorsal carapace are given in Table 2. Measurements of total length and width were made exclusive of the spines.

Table 2.—Measurements (in mm) taken on specimens of *Trichopeltarion levis* new species. L = total carapace length; WT = total carapace width; WR = rostral width; WP = posterior width.

Specimen number	L	WT	WR	WP
MSNM i25533	12.8	12	3	4.9
MSNM i25524	21.2	20.9	3.9	11.4
MSNM i25528	Broken	Broken	Broken	Broken
GHUNLPam 25.041	9.7	ca. 8.8	2.3	4.3
CM 52504	Broken	25.7	5.7	Broken
GHUNLPam 25.039	17.9	16.3	3.7	9.8
GHUNLPam 25.040 Holotype	20.8	21.7	4	10.9
GHUNLPam 25.042	18.9	18.7	3.6	9.2

**Discussion.**—Species of *Trichopeltarion* are distinguished from one another on the basis of the carapace outline; the degree to which carapace regions are distinctly delimited by grooves; the nature of ornamentation of the carapace, exclusive of spines and nodes; and the form and development of spines on the margins and on the surface of the carapace (Table 3). Although *Trichopeltarion levis* bears all the characters allying it with the genus, its morphology is clearly different from all previously known species. Thus, its identity as a new species is certain. The plexus of characters: circular outline, 19 simple marginal spines including the rostral and orbital spines, smooth carapace surface separating smooth tubercles, and only moderately-defined regions, is exhibited by no other described species. The most similar form is *T. merrinae* Schweitzer and Salva, 2000, from the late Miocene of New Zealand; however, *T. merrinae* has an elongate carapace with both simple and complex marginal spines and a granular carapace surface between granular tubercles. Both species have a large number of marginal spines compared to other species of the genus, including three pairs on the posterolateral margin.

Superfamily Xanthoidea MacLeay, 1838  
Family Pilumnidae Samouelle, 1819

**Discussion.**—Several advances have recently been made in assigning fossil genera to the Pilumnidae, a family which has historically been largely overlooked by paleontologists who have favored placement of taxa in the Xanthidae *sensu lato* MacLeay, 1838 (Glaessner, 1969). Schweitzer (2000) placed several genera into the Pilumnidae *sensu lato* with no attempt at placing them into subfamilies; those genera included *Actumnus* Dana, 1851; *Galene* de Haan, 1833; *Galenopsis* A. Milne Edwards, 1865; *Glabropilumnus* Balss, 1932; *Lobogalenopsis* Müller and Collins, 1991; *Pilumnominus* Müller and Collins, 1991; *Pilumnopus* A. Milne Edwards, 1863; *Pilumnus* Leach, 1815; and *Pulalius* Schweitzer et al., 2000. Davie (2002) has provided useful diagnoses for extant members of the family and several of the constituent subfamilies.

Schweitzer (2000) discussed the Pilumnidae in the fossil record and suggested methods by which to assign

fossils to the family. The most prominent characters that are preservable in the fossil record that can be used to assign some genera to the family are the pronounced longitudinal vaulting of the carapace in the anterior third; long protogastric and hepatic regions; carapace width not much greater than length; medially notched front; poorly defined regions; anterolateral margin being shorter than posterolateral margin; arcuate epibranchial regions; and possession of 2–4 small, usually blunt, anterolateral spines.

These characters best fit the Galeninae Alcock, 1898, and the Pilumninae Samouelle, 1819, as defined by Davie (2002). As stated by Schweitzer (2000, p. 736), “this combination of characters is diagnostic only for some pilumnids. Therefore, the diagnosis should allow some fossil specimens to be assigned to the Pilumnidae, although it will not be diagnostic for all members of the family.” In fact, the Halimedinae Alcock, 1898; Rhizopinae Stimpson, 1858; Calmaniinae Števčić, 1991, and Eumedoninae Dana, 1853, diverge markedly from this diagnosis (Davie, 2002). The Galeninae possess very poorly developed regions and lack acute spines on the anterolateral margins. Members of the Pilumninae usually have well-defined regions and have acute spines on the anterolateral margins (Davie, 2002).

The Galeninae embraces only one extant genus, *Galene* (Davie, 2002), which has an Indo-Pacific distribution and is also known in the fossil record from Pliocene and Pleistocene rocks of that region (Glaessner, 1969). The Miocene *Galene proavita* Glaessner, 1960, has recently been moved to *Carcinoplax*, a decision with which we concur (Karasawa and Kato, 2003a). *Pulalius* and *Tumidocarcinus* are quite similar to extant *Galene* in many regards; Schweitzer (2000, p. 736) discussed the remarkable similarity between Eocene and Oligocene *Pulalius* and the extant *Galene*. Species of *Tumidocarcinus* are also quite similar to *Galene* in possessing a four-lobed front, sub-equal anterolateral and posterolateral margins or anterolateral margins somewhat longer than the posterolateral margins, weakly developed carapace regions, a strongly vaulted carapace, and a similar shape and arrangement of carapace regions. *Paratumidocarcinus* appears to be quite similar in shape and ornamentation to *Tumidocarcinus*, based upon the illustration and brief description (Martins-Neto, 2001). *Baricarcinus* new genus is herein allied with these genera due to its possession of a highly longitudinally vaulted carapace, weakly defined regions, blunt protuberances on the anterolateral margins, long protogastric and hepatic regions, and anterolateral margins shorter than posterolateral margins. Thus, it appears that these fossil species are best allied with *Galene*; however, work in progress by one us (CS) is addressing that issue.

Aguirre-Urreta et al. (1995) named a new species of *Tumidocarcinus*, *T. forsteri*. It does not belong to the genus for several reasons. Species of *Tumidocarcinus* are extremely large and inflated; *T. forsteri* exhibits neither



Table 3.—Species of *Trichopeltarion* and features of the dorsal carapace of each. SPINE = nature of the ornament of individual spines; SURF = ornamentation of dorsal carapace surface; REG = definition of dorsal carapace regions; TUBS = nature of carapace tubercles; # = number of anterolateral spines; S = smooth; G = granular; R = reduced.

Species	Age	Outline	Spine	SURF	REG	TUBS	#
<i>T. nobili</i> A. Milne Edwards, 1880	Recent	Circular	Complex	G	Moderate	G	15
<i>T. alcocki</i> (Doflein, 1903)	Recent	Elongate	Simple	G	Distinct	G	15
<i>T. balssi</i> (Rathbun, 1932)	Recent	Circular	Complex	G	Distinct	G	13?
<i>T. berghlundorum</i> Schweitzer and Feldmann, 1999	I. Olig.-early Miocene	Elongate	Simple	S	Distinct	G	15
<i>T. corallinus</i> (Faxon, 1893)	Recent	Elongate	Simple	S	Indistinct	G	15
<i>T. crosneri</i> (Guinot, 1986)	Recent	Elongate	Complex	G	Distinct	G	15
<i>T. decorus</i> (Rathbun, 1945)	Miocene	Circular	Simple	G	Moderate	?	?
<i>T. elegans</i> (Guinot and Sakai, 1970)	Recent	Circular	Simple	G	Indistinct	G	13
<i>T. fantasticum</i> Richardson and Dell, 1964	Recent	Elongate	Complex	G	Moderate	G	15
<i>T. glaucus</i> (Alcock and Anderson, 1899)	Recent	Elongate	Complex	G	Distinct	G	15
<i>T. granulosa</i> (Schweitzer and Salva, 2000)	Miocene	Elongate	Simple	G	Distinct	S	15
<i>T. greggi</i> Dell, 1969	I. Mio.	Circular	Complex	G	Indistinct	R	15
<i>T. huziokai</i> (Imazumi, 1951)	Miocene	Circular	Complex	G	Distinct	S	15
<i>T. inflatus</i> (Kato, 1996)	Miocene	Circular	Simple	S	Distinct	G	13
<i>T. intesi</i> (Crosnier, 1981)	Recent	Elongate	Complex	G	Moderate	G	13
<i>T. merrinae</i> Schweitzer and Salva, 2000	late Miocene	Elongate	Both	G	Moderate	G	19
<i>T. moosai</i> (Guinot, 1989)	Recent	Elongate	Simple	G	Moderate	G	15
<i>T. ovalis</i> (Anderson, 1896)	Recent	Circular	Simple	G	Moderate	G	15
<i>T. sagamiensis</i> (Rathbun, 1932)	Recent	Elongate	Complex	G	Distinct	G	19
<i>T. spinulifer</i> (Rathbun, 1898)	Recent	Elongate	Complex	G	Moderate	G	17
<i>T. wardi</i> Dell, 1968	Recent	Elongate	Complex	G	Distinct	G	15
<i>T. levis</i> new species	Eocene	Circular	Simple	S	Moderate	S	19

feature. Carapace regions are moderately well defined in *T. forsteri*, and the carapace is flattened, neither of which are possessed by any other species of *Tumidocarcinus*. The orbits of *T. forsteri* are small and narrowly spaced, while those in other *Tumidocarcinus* are larger and more broadly spaced. The front is quadrilobed in *Tumidocarcinus*, while in *T. forsteri*, it is axially sulcate and appears to be triangular and downturned. The carapace of *T. forsteri* is flattened, lacking the pronounced vaulting of the carapace typical of *Tumidocarcinus* and other members of the subfamily. Thus, it should be removed from *Tumidocarcinus*. However, placement of this species into a genus and family must await examination of the type specimens.

Alphonse Milne Edwards (1865, p. 316) considered *Galenopsis* to be quite similar to *Galene* (= *Galena* in his work) in its smooth carapace, quadri-lobed front, short anterolateral margins as compared to the posterolateral margins, and blunt spines or protuberances on the anterolateral margins. Schweitzer (2000) concurred as did Karasawa and Kato (2003a). However, *Galenopsis* cannot be placed within the Pilumnidae, because the abdomen of males extends beyond the anterior edge of the chelipeds (see A. Milne Edwards, 1865, pl. 8, fig. 2a), which is not characteristic of the Pilumnidae. In addition, the anterolateral margins of *Galenopsis* are much shorter than those of most Pilumnidae, and the carapace is much more flattened than in most authentic pilumnids.

*Galenopsis* appears to be best placed within the Goneplacidae MacLeay, 1838, as suggested by Glaessner (1969), based upon its flattened, rectangular carapace; poorly defined regions; broad fronto-orbital width; short

anterolateral margins with small, sharp spines; notched, straight front; and free male abdominal somites. The subfamily Euryplacinae Stimpson, 1871, accommodates *Galenopsis* well. That subfamily is characterized by poorly defined carapace regions; a straight front with a median notch; broad fronto-orbital width; a distinct supraorbital angle; a short anterolateral margin with 2–5 spines; broadened sternum and a sterno-abdominal cavity reaching the anterior edge of sternite 4; all male abdominal somites free and somites 4–6 much narrower than 3, a telson longer than wide; and an abdomen typically triangular in shape (Davie, 2002; Karasawa and Kato, 2003a). The preserved features of species of *Galenopsis* exhibit features of the subfamily; thus, the genus is placed into the subfamily with confidence. *Galenopsis* is known from Eocene to Oligocene rocks of Europe, east Africa, and India and questionably from Pliocene rocks of Fiji (Glaessner, 1969); these occurrences do not expand the geologic or geographic range of the subfamily as defined by Karasawa and Kato (2003a).

Karasawa and Kato (2003a) performed a phylogenetic analysis on fossil and selected extant members of the Goneplacidae, and they reevaluated those genera previously referred to the Goneplacidae, placing some into the Pilumnidae. In so doing, they assigned *Maingrapsus* Tessier et al., 1999, and *Paracoralliocarcinus* Tessier et al., 1999, to the Pilumnidae, allied with *Georgeoplax* Türkay, 1983. Karasawa and Kato (2003b) indicated that *Georgeoplax* does not have an auxiliary plate on sternite 8, suggesting that it does not belong within in the Chasmocarcininae Serène, 1964. However, Davie (2002) has placed *Georgeoplax* in the Chasmocarcininae of the

Goneplaeidae; thus, more work will need to be done to resolve the placement of *Georgeoplax*, *Maingrapsus* and *Paracorallicarcinus*. Members of the Chasmocarcininae possess an auxiliary plate on sternite 8; if that feature were to be assessed in specimens of *Maingrapsus* and *Paracorallicarcinus*, it would help to resolve the problem.

#### Genus *Baricarcinus*, new genus

*Included Species*.—*Baricarcinus mariae* new species, by monotypy.

*Diagnosis*.—as for species.

*Etymology*.—The genus name is taken from the Greek *karkinos*, meaning crab, and Bariloche, Río Negro Province, Argentina, a resort town and the largest town near the type locality of the new genus in Patagonia, Argentina.

*Description*.—as for species.

*Occurrence*.—*Baricarcinus* is known only from the occurrence reported herein.

*Discussion*.—*Baricarcinus* is represented by two specimens which are moderately well preserved. While they superficially resemble many members of the Pilumnidae and the Xanthoidea, their morphology cannot be embraced by any existing genus. The new specimens are quite similar to species of *Tumidocarcinus*; however, in *Tumidocarcinus*, the carapace is extremely inflated overall; the front is distinctly quadrilobed; the anterolateral margins and posterolateral margins are subequal; and the fronto-orbital width occupies about 50 percent the maximum carapace width. In the new material, the carapace is not greatly inflated overall; the front is bilobed; the anterolateral margin is markedly shorter than the posterolateral margins; and the fronto-orbital width occupies about 65 percent the maximum carapace width. Members of *Galene* have acute spines on the anterolateral margins, while the new material has very weak blunt protuberances. In species of *Galene*, the fronto-orbital width occupies 40 percent the maximum carapace width, while in the new material, the fronto-orbital width is 65 percent the maximum carapace width. The frontal width in species of *Galene* is much narrower than that of the new material, 20 and 37 percent respectively. The new material is easily distinguished from *Pulalius*, in which the carapace regions are moderately well marked, the orbits are fissured, the front is distinctly quadri-lobed, and the fronto-orbital width is much narrower. The new material has none of those attributes. Thus, the new material is placed within a new genus.

#### *Baricarcinus mariae*, new species (Fig. 7A–B, D–E)

*Types*.—Holotype, GHUNLPam 25.003; paratype, GHUNLPam 25.004; CM.52525, cast of GHUNLPam 25.003.

*Diagnosis*.—Carapace not much wider than long, L/W about 0.85, widest at position of last anterolateral protuberance; regions not well-defined; strongly vaulted

longitudinally, especially in anterior third; front smoothly bilobed; orbits circular, entire, fronto-orbital width about 65 percent maximum carapace width; anterolateral margin shorter than posterolateral, with three blunt protuberances, third largest; epibranchial regions arcuate, with medial swelling and swelling paralleling margin of mesogastric region.

*Etymology*.—The trivial name honors Dr. Maria B. Aguirre-Urreta, Universidad de Buenos Aires, in recognition of her work on southern hemisphere decapods.

*Description*.—Carapace not much wider than long, L/W about 0.85, widest at position of last anterolateral protuberance, at about 60 percent distance posteriorly on carapace; regions not well defined; surface appearing to have been weakly granular before weathering; moderately vaulted transversely, strongly vaulted longitudinally, especially in anterior third.

Front about 37 percent maximum width, with smooth notch at midline, lateral edges bordering orbits rounded, produced well in advance of orbits, directed downward. Fronto-orbital width about 65 percent maximum carapace width; orbits circular, directed anterolaterally, entire, upper margin weakly rimmed, outer-orbital angle sharp but not produced. Anterolateral margin convex; shorter than posterolateral margin, measured between outer-orbital angle and last anterolateral protuberance about 45 percent maximum length; initially straight; straight segment followed by two blunt, weak protuberances and third, better developed, protuberance at anterolateral corner. Posterolateral margin weakly convex, entire, weak reentrant at posterolateral corner; length measured between last anterolateral protuberance and posterolateral reentrant about 60 percent maximum carapace width. Posterior margin nearly straight, rimmed, about half maximum carapace width.

Epigastric regions very weakly developed, slightly elevated above remainder of carapace; protogastric regions long, weakly inflated posteriorly; mesogastric region with long, slender anterior process, widening posteriorly, very poorly marked posteriorly; urogastric region depressed, not well-differentiated; cardiac region inflated, especially transversely across midlength of region, hexagonal in shape; intestinal region not well defined.

Hepatic region long, weakly expressed; epibranchial region arcuate, extending from base of last anterolateral protuberance to lateral margins of mesogastric region, with medial swelling; oblong swelling directed obliquely, parallel and adjacent to margin of mesogastric region; remainder of branchial regions undifferentiated, with weak swelling positioned adjacent to midlength of posterolateral margin.

Remainder of carapace and appendages unknown.

*Measurements*.—Measurements (in mm) were taken on the dorsal carapace of GHUNLPam 25.003 and 25.004 respectively of *Baricarcinus mariae*. Maximum width: 12.2, 11.0; maximum length: 10.4, 9.5; fronto-orbital width, 7.8, 7.2; frontal width, 4.8, 3.9; posterior width, 5.6, 5.2; length to position of maximum width, 6.0, 5.4; length of anterior margin measured between outer-orbital angle and last anterolateral protuberance: 4.9, 4.0; posterolateral width measured between last anterolateral protuberance and posterolateral reentrant: 6.7, 5.2.

*Discussion*.—The carapace of the new species is much smaller than is typical for other forms that appear to be closely related. However, all other aspects conform well to the diagnosis for the family. Only two specimens are known, suggesting either that the species was relatively uncommon compared to the other taxa reported herein or that it inhabited a niche or exhibited a lifestyle that reduced its possibility of being fossilized.



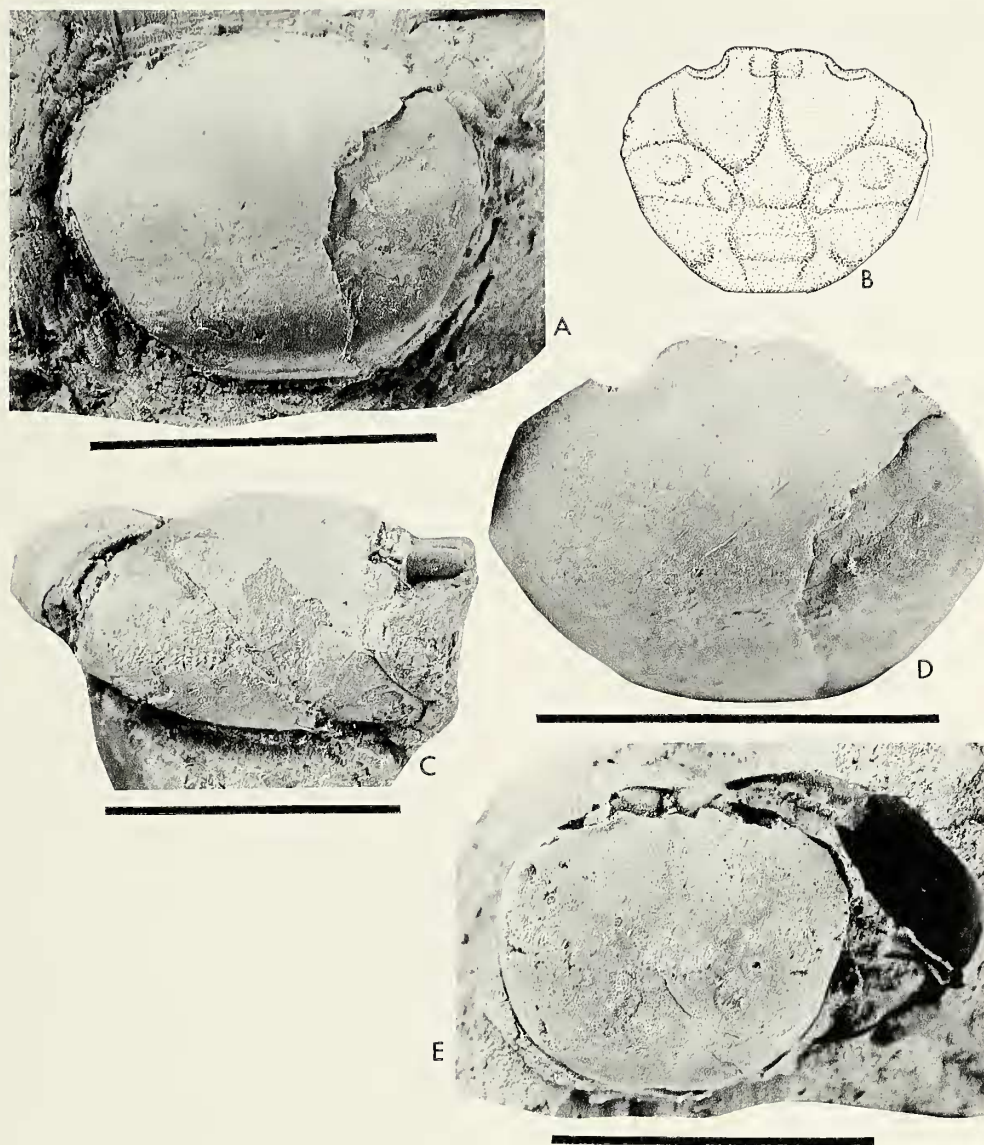


Fig. 7.—Xanthoidea. A. Dorsal carapace of *Baricarcinus mariae* new genus and species, holotype GHUNLPam 25.003; B. Composite line drawing of *Baricarcinus mariae*; C. Indeterminate xanthoid chela, MSNM i23017; D. *Baricarcinus mariae*, oblique anterior view of dorsal carapace, showing front and orbits, holotype GHUNLPam 25.003; E. Dorsal carapace of *Baricarcinus mariae*, paratype GHUNLPam 25.004. Scale bars equal to 1 cm.

Superfamily Pinnotheroidea de Haan, 1833

Family Pinnotheridae de Haan, 1833

Subfamily Asthenognathinae Stimpson, 1858

*Included Genera*.—*Asthenognathus* Stimpson, 1858;  
*Tritodynamia* Ortmann, 1894.

*Diagnosis*.—Carapace trapezoidal, wider than long, average length/width about 0.70, typically with a range of 0.54–0.87, typically no higher than 0.79; lateral margins usually steep; regions usually not well-defined; front narrowing distally, deflexed, axially sulcate, usually bilobed, not extending or only slightly extending beyond orbits; orbits shallow; anterior margin usually entirely occupied by orbits, fronto-orbital width to width ratio usually about 0.50, ranging from 0.37–0.70 but typically

no higher than 0.59; anterolateral and posterolateral margins confluent; posterolateral reentrant large; posterior width about half maximum carapace width, ranging from 0.44–0.64; fronto-orbital width to posterior width ratio usually about 1.00, with outliers at about 0.80; branchial region often with inflated epibranchial ridge; sternite 4 without anterior projections (after Schweitzer and Feldmann, 2001a).

*Discussion*.—Alcock (1900) suggested an arrangement of several subfamilies within the Pinnotheridae including the Asthenognathinae Stimpson, 1858. Pohle and Marques (1998) performed a phylogenetic analysis on the Pinnotheridae, based primarily upon gill structure, and rejected most of these subfamily groupings, including the

Asthenognathinae. In their analysis, *Asthenognathus* formed a monophyletic group of its own (Pohle and Marques, 1998). However, because strong morphological evidence suggests that at least *Asthenognathus* and *Tritodynamia* are closely related (Schweitzer and Feldmann, 1999), we maintain those two genera within the subfamily. Števcic (1996) had previously suggested the removal of *Mortensenella* Rathbun, 1909, and *Hapalonnatus* de Man, 1879, from the Asthenognathinae. Other genera included in the subfamily by Schweitzer and Feldmann (2001a) were not found to be closely related to *Asthenognathus* (Pohle and Marques, 1998) and will need to be evaluated independently, which is beyond the scope of this paper. Interestingly, Pohle and Marques (1998) found *Asthenognathus* to be one of the basal-most, or least derived, groups within the Pinnotheridae, which is supported by its antiquity. *Asthenognathus* is one of the oldest known pinnotherid genera in the fossil record, with Oligocene records in Washington, USA (Schweitzer and Feldmann, 1999) and the new occurrence herein. Other, older pinnotherid occurrences include *Viapinnixa* Schweitzer and Feldmann, 2001a, from the Danian of Greenland (Collins and Rasmussen, 1992) and the Eocene of Mexico (Vega et al., 2001). The Eocene occurrence of *Pinnixa* White, 1846, reported by Glaessner (1969) has since been referred to the Hexapodidae (Schweitzer et al., 2000).

The subfamily diagnosis herein is based upon *Asthenognathus* and *Tritodynamia*, which are very similar in terms of dorsal carapace characters (Schweitzer and Feldmann, 1999). Features of the new species described here, *Asthenognathus microspinosus*, as well as *A. urretae* Schweitzer and Feldmann, 2001a, expand the definition of the genus, and thus the subfamily, as defined by Schweitzer and Feldmann (2001a). Schweitzer and Feldmann (2001a) diagnosed the subfamily as being characterized by a length/width (L/W) ratio of about 0.69, ranging from 0.54–0.79, and *Asthenognathus* as having a L/W of about 0.66. The new species falls outside the range of both the subfamily and the genus, with a L/W of about 0.87 on average. Extant species of *Asthenognathus* have a fronto-orbital width to width ratio of 0.55, as does the new species, while two other fossil members, *A. cornishorum* Schweitzer and Feldmann, 1999, and *A. urretae*, have ratios that are much higher, 0.70. Thus, the range of the fronto-orbital width to width ratio in both the subfamily and the genus is expanded as well.

#### Genus *Asthenognathus* Stimpson, 1858

*Type Species*.—*Asthenognathus inaequipes* Stimpson, 1858, by original designation.

*Included Species*.—*Asthenognathus atlanticus* Monod, 1933 (extant); *A. cornishorum* Schweitzer and Feldmann, 1999 (fossil); *A. gallardoi* Serène and Soh, 1976 (extant); *A. globosa* (Karasawa, 1990) as *Tritodynamia* (fossil); *A. hexagonum* Rathbun, 1909 (extant); *A. microspinus* new

species (fossil); *A. urretae* Schweitzer and Feldmann, 2001a (fossil).

*Diagnosis*.—Carapace trapezoidal, length to width ratio ranging from 0.63–0.87, averaging about 0.71; front downturned, axially sulcate, bilobed in extant forms, straight in fossil forms, about 20 percent maximum carapace width; fronto-orbital width to width ranging from 0.45–0.70, averaging about 0.59; anterolateral and posterolateral margins confluent; fronto-orbital width to posterior width about 1.00 in extant forms, about 0.80 in fossil forms; posterior width about half maximum carapace width; epigastric region square, inflated; cardiac region well-defined; branchial region may have broadly inflated epibranchial region forming a ridge, may be developed as a narrow ridge just posterior to epibranchial region, or may lack ornamentation.

*Discussion*.—Schweitzer and Feldmann (2001a) reviewed the genus and the occurrences of the subfamily Asthenognathinae in the fossil record. In addition to the characters discussed above under the subfamily, some fossil species of *Asthenognathus* differ from extant species in some ways. Extant species of *Asthenognathus*, as well as other extant members of the subfamily, have fronto-orbital width to posterior width ratios of about 1.00, while the three fossils for which this measure is available have much lower ratios, 0.74–0.85. Schweitzer and Feldmann (2001a) found that the ratio of the fronto-orbital width to posterior width was an important character in differentiating between members of the Hexapodidae Miers, 1886, and other decapods with similar dorsal carapace morphology. This is, therefore, a significant difference between the fossil and extant species. In addition, extant members of *Asthenognathus* have a bilobed front that is axially sulcate. The bilobed nature ranges from being very distinct in dorsal view in *A. inaequipes* to less distinctive in *A. atlanticus*. In the fossil species in which the front is preserved, it is straight and axially sulcate. Thus, there appears to be a trend from straight fronts to more distinctly bilobed fronts through time. Two fossil members of *Asthenognathus*, *A. urretae* and *A. microspinus* new species, have a broad epibranchial ridge extending from the anterolateral corner obliquely to the cardiac region. The extant *A. atlanticus* has a very narrow ridge in the branchial area, appearing to be just posterior to the position of the epibranchial region (Monod, 1956, p. 384, fig. 541). Further, *A. inaequipes* appears to have a broadly swollen epibranchial region, although it is not developed into a distinctive ridge as in the two fossil species (Sakai, 1976, pl. 203). Thus, the development of the epibranchial ridge is variable in both extant and fossil species of the genus.

All of these exceptions indicate that *Asthenognathus* as currently understood is a variable genus. Considerable variation exists in the length/width, fronto-orbital width to width, and fronto-orbital to posterior width ratios as well as in the nature of the front and the epibranchial region. As shown, however, there are gradations in the nature of



Table 4.—Carapace ratios and other characteristics of species of all species of *Asthenognathus*, except *A. hexagonum* Rathbun, 1909, for which information is not known, and *A. gallardoi* Serène and Soh, 1976. \* Measurements taken from specimens illustrated in Monod (1956). L = maximum length; W = maximum width; FOW = fronto-orbital width; PW = posterior width; F = frontal (rostral) width.

Species	L/W	FOW/W	FOW/PW	PW/W	F/W	Front	Epibranchial region
<i>A. atlanticus</i> Monod, 1933, specimen 1*	0.67	0.59	1.07	0.55	0.25	Bilobed	narrow ridge
<i>A. atlanticus</i> Monod, 1933, specimen 2*	0.73	0.56	1.29	0.44	0.27	Bilobed	narrow ridge
<i>A. atlanticus</i> Monod, 1933, specimen 3*	0.67	0.58	1.00	0.58	0.24	Bilobed	narrow ridge
<i>A. cornishorum</i> Schweitzer and Feldmann, 1999	0.71	0.7	0.8	0.51	0.15	Unknown	none
<i>A. globosa</i> (Karasawa, 1990)	0.73	—	—	—	0.2	Unknown	none
<i>A. inaequipes</i> Stimpson, 1858	0.69	0.45	1.00	0.45	0.17	Bilobed	broad ridge, weak
<i>A. microspinus</i> new species	0.87	0.54	0.85	0.54	0.23	Straight	broad ridge
<i>A. urretae</i> Schweitzer and Feldmann, 2001a	0.66	0.7	0.74	0.57	0.16	Straight	broad ridge

the front and epibranchial regions. Further, examination of the characters of each species (Table 4) demonstrates that there is no clear means by which to separate the genus into two or more genera. There is too much overlap in characters between various species.

Further complicating the effort is the fact that members of the Chasmocarcininae Serène, 1964 of the Goneplacidae MacLeay, 1838, have dorsal carapace morphologies almost identical to asthenognathines (Schweitzer and Feldmann, 2001a). The best means by which to differentiate members of the Chasmocarcininae and the Asthenognathinae is by the nature of the sternum; chasmocarcinines have a distinctive supplementary plate between sternites 7 and 8 which is unique to the group. Without the sternum, it may be nearly impossible to determine if species are chasmocarcinines or asthenognathines. The fossil specimens discussed here as well as those referred to *A. cornishorum* and *A. urretae* do not have the supplementary plate and are clearly not members of the Chasmocarcininae. We opt to retain all of the fossil and extant species currently assigned to *Asthenognathus*, even in light of the considerable variation in various characters of the dorsal carapace (Table 4). We believe that this will best demonstrate the affinities of these animals, which are clearly closely related and are demonstrably not members of the Chasmocarcininae.

Thus far, the oldest known species of the genus is *Asthenognathus microspinus*, middle Oligocene in age, described here. *Asthenognathus urretae* was reported from the Centinela Formation, near Calafate, Argentina, then thought to be Eocene in age (Casadio, Feldmann et al., 2000; Schweitzer and Feldmann, 2001a). Newer information suggests that the Centinela Formation is most likely late Oligocene–early Miocene in age (Casadio et al., 2000; Guerstein et al., in press), making that species about the same age as *A. cornishorum* from Washington, USA (Schweitzer and Feldmann, 1999). *Asthenognathus globosa* is known from early Miocene rocks in Japan (Karasawa, 1990; 1993). Thus, the genus displayed an amphitropical distribution throughout its early history. The new species does not greatly expand the geographic range of the genus. Extant members of the genus inhabit the Atlantic Ocean from France to North Africa (Monod, 1956; Manning and Holthuis, 1981), and the Indo-Pacific

(Rathbun, 1909; Sakai, 1976). The early amphitropical distribution and the modern tropical distribution suggest that the genus was dispersed via Tethyan routes and currently displays a relict Tethyan distribution.

#### *Asthenognathus microspinus*, new species (Fig. 8)

**Types.**—Holotype GHUNLPam 25.043, paratypes GHUNLPam 25.044–25.073; paratypes MSNM i23463–i23468; paratypes CM 52508–52513; CM52519, cast of MSNM i25468; CM 52520, cast of MSNM i28466; CM 52521, cast of MSNM i25463; CM52526, cast of GHUNLPam 25.062; CM 52527, cast of GHUNLPam 25.065; CM 52528, cast of GHUNLPam 25.049; CM 52529, cast of GHUNLPam 25.052; CM 52530, cast of GHUNLPam 25.061.

**Diagnosis.**—Carapace only slightly wider than long, L/W = 0.87; surface finely granular, granules coarsest near posterior margin; rostrum deflexed, straight, axially sulcate; anterolateral margin with tiny, closely spaced spines; epigastric region broadly inflated into ridge.

**Etymology.**—The trivial name is derived from the Greek words *mikros*, meaning small, and *spinos*, meaning spine, referring to the tiny spines on the anterolateral margin, unique among members of the genus.

**Description.**—Carapace trapezoidal, slightly wider than long, L/W = 0.87, widest just anterior to posterolateral reentrant; flattened transversely and moderately vaulted longitudinally; surface granular, granules coarsest posteriorly.

Fronto-orbital width occupying entire anterior margin of carapace; rostrum downturned, extending slightly beyond orbits, maintaining width along entire length, anterior margin straight, axially sulcate dorsally, about 23 percent maximum carapace width; orbits directed slightly axially, rimmed, margins sinuous, fronto-orbital width about 54 percent maximum carapace width; frontal width to fronto-orbital width ratio about 0.43.

Anterolateral and posterolateral margins continuous, anterolateral portion ornamented by small, sharp, closely spaced spines; posterolateral reentrants large, smooth, rimmed; posterior margin straight, rimmed, about 63 percent maximum carapace width, fronto-orbital width about 85 percent posterior width.

Epigastric regions square, markedly inflated; mesogastric region well-defined posteriorly, anterior process weakly marked; protogastric and hepatic regions poorly differentiated from one another; urogastric region well-defined, long, with concave margins; cardiac region triangular, apex directed posteriorly, round swellings at each point of triangle; intestinal region flattened, poorly differentiated. Epibranchial region inflated to form a ridge, beginning at anterolateral corner and

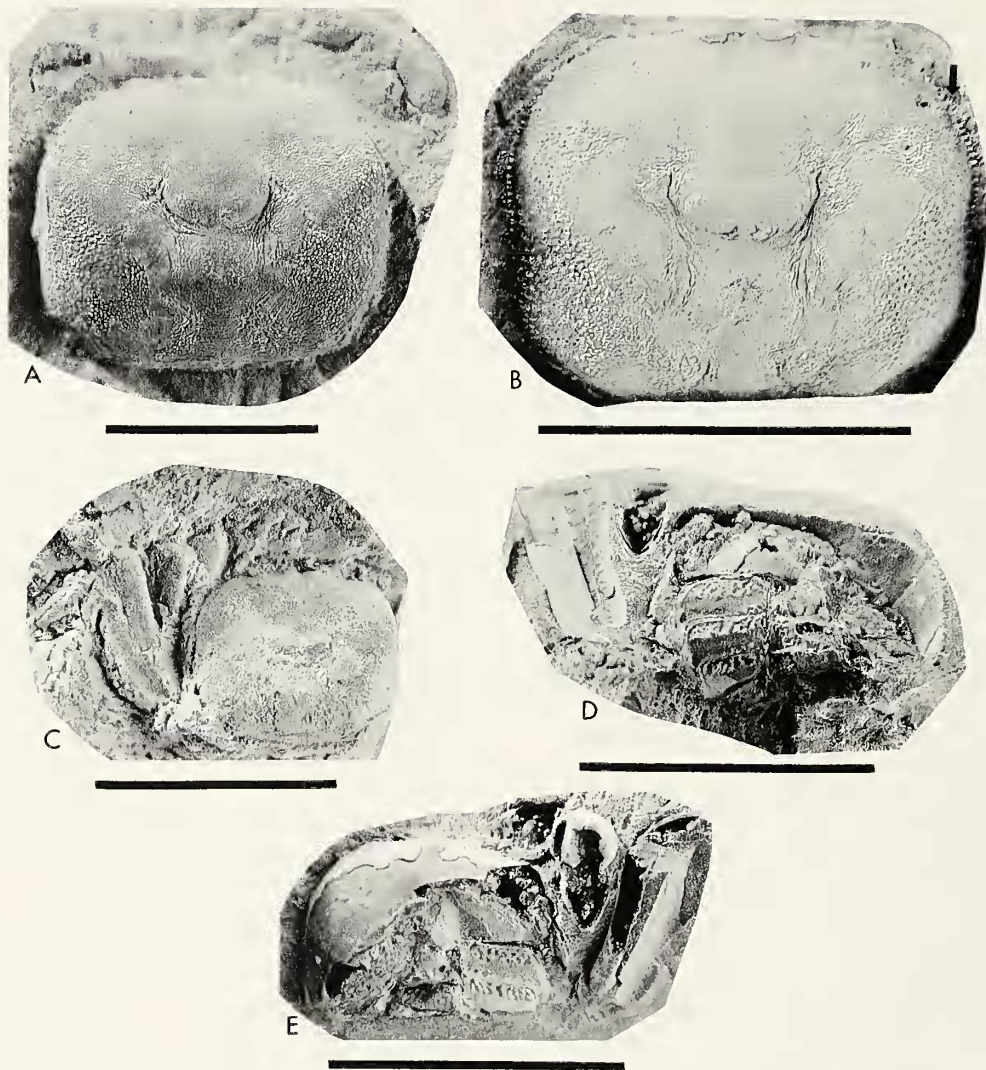


Fig. 8.—*Asthenognathus microspinus*. A. Dorsal carapace, paratype MSNM i25466; B. Dorsal carapace, holotype, GHUNLPam 25.043, arrows indicate tiny spines on anterolateral margin; C. Dorsal carapace and appendages, paratype GHUNLPam 25.061; D. Ventral view of sternites and portion of male abdomen, paratype GHUNLPam 25.047 (part); E. Ventral view of sternites, GHUNLPam 25.047 (counterpart). Scale bars equal to 1 cm.

extending to anterior margin of cardiac region; remainder of branchial region undifferentiated.

Thoracic sternites 4–6 with parallel upper and lower margins, each sternite granular anteriorly. Chelipeds short, chelae stout; meri of pereopods 2 and 3 long, slender.

**Measurements.**—Measurements (in mm) taken on specimens of *Asthenognathus microspinus* are in Table 5.

**Discussion.**—*Asthenognathus microspinus* new species closely resembles the characteristics that define the genus with a few exceptions, as discussed above. Distinctive features of the new specimens demonstrate that they should be considered as a new species. The posterolateral re-entrants of *A. microspinus* are deeper and better-defined than those in other species. Undoubtedly, the most distinguishing difference between *A. microspinus* and all other species of the genus is the

presence of small spines on the anterolateral margin (GHUNLPam 25.043). These are unique among members of the genus.

The cardiac region of *A. microspinus* new species is transversely hexagonal, while that of other species is semi-circular in shape (Monod, 1956; Karasawa, 1993; Schweitzer and Feldmann, 2001a). The mesogastric region in *A. microspinus* is well-defined by grooves posteriorly and poorly defined anteriorly, while *A. inaequipes* and *A. atlanticus* have better defined anterior portions of the mesogastric region (Monod, 1956; Sakai, 1976). The epibranchial region of *A. microspinus* is broadly inflated and ridge-like, while *A. atlanticus*, *A. cornishorum*, and *A. inaequipes* lack this quality (Monod, 1956; Schweitzer and Feldmann, 1999; Schweitzer and Feldmann, 2001a). *Asthenognathus cornishorum* pos-



Table 5.—Measurements (in mm) taken on specimens of *Asthenognathus microspinus* new species.

Specimen	Width	Length	Posterior width	Fronto-orbital width	Frontal width
GHUNLPam 250.49	11.4	9.0	6.4	—	—
CM 52511	10.2	8.7	5.7	5.1	2.2
CM 52510	8.1	7.7	—	—	—
CM 52508	11.1	10.1	7.0	—	—
CM 52513	9.5	7.7	5.9	—	—
GHUNLPam 25.043 Holotype	12.8	11.1	7.8	6.8	2.7
MSNM i25468a	11.5	10.0	7.1	6.0	2.6
GHUNLPam 25.065	11.4	10.3	—	5.4	2.5
MSNM i25463	9.0	7.8	5.7	4.8	2.2
GHUNLPam 25.044	9.2	8.2	5.9	5.1	2.5
MSNM i25465	11.3	9.4	6.8	—	—
MSNM i25466	12.6	10.8	8.4	6.5	2.6
GHUNLPam 25.061	8.2	7.6	4.8	—	—
GHUNLPam 25.062	11.2	9.5	7.1	—	—
GHUNLPam 25.045	8.1	7.0	5.4	4.7	2.0
GHUNLPam 25.046	7.7	7.3	6.0	5.0	1.9

sesses a row of granules parallel to the posterior margin (Schweitzer and Feldmann, 1999), not present on the new species. The carapace of *A. urretae* is ornamented with setal pits, not present on the new species, and *A. urretae* possesses a tiny spine in the posterolateral re-entrant not present in the new species. The carapace of *A. globosa* is more densely granular and the granules are larger than the granules present on the new species (Karasawa, 1990, 1993).

#### Indeterminate Cheliped (Fig. 7C)

*Material Examined*.—Specimen MSNM i23017.

*Description*.—Manus of cheliped longer than high, H/L about 0.65, becoming higher distally, bulbous, moderately vaulted longitudinally and highly vaulted from upper to lower margin; proximal margin oriented obliquely, making about 70 degree angle with lower margin; upper and lower margins convex; distal margin appearing to be relatively straight.

Fixed finger extending in straight line from manus, lower margin straight, narrowing markedly distally. Movable finger narrowing distally.

Carpus of cheliped bulbous, not much longer than high, H/L about 0.90; proximal margin strongly convex; lower margin short, convex; upper margin weakly convex; distal margin nearly straight, rimmed.

Remainder of cheliped unknown.

*Measurements*.—Measurements, in mm, taken on MSNM i23017: maximum length of manus (L), 12.5; maximum height of manus (H), 8.1; maximum length of carpus (L), 6.4; maximum height of carpus (H), 5.8.

*Discussion*.—The material is insufficient to make any taxonomic judgement. More material will be necessary to resolve the identity of this specimen; we report it because it differs from all other material described herein and thus represents a separate taxon.

## DISCUSSION

The number of fossil decapod species reported from Argentina has increased dramatically in recent years (Feldmann et al., 1995; Schweitzer and Feldmann, 2000a, b, c, 2001a). Interestingly, the faunas of individual rock units, even those of roughly equivalent age, are remarkably different from one another. Of the decapods described from localities in the Late Oligocene–early Miocene Centinela Formation near Estancia 25 de Mayo, near Calafate, Santa Cruz Province, three genera, *Asthenognathus*, *Munida*, and *Proterocarcinus*, are shared with the fauna of the middle Oligocene Río Foyel Formation, collected near Bariloche, about 500 km to the north. Notably, the Río Foyel Formation decapods are just as similar to the fauna of the late Oligocene–early Miocene Pysht Formation of Washington, USA; the two units share three genera, including *Asthenognathus*, *Callianopsis*, and *Trichopeltarion* (Schweitzer-Hopkins and Feldmann, 1997; Schweitzer and Feldmann, 1999).

Clearly this pattern deserves detailed investigation, in progress by two of us (RF and CS); at the least, this pattern of shared decapod genera supports the Oligocene age suggested for the Patagonian rock units.

Two species described herein represent the oldest known occurrences of their respective genera, *Trichopeltarion levis* and *Asthenognathus microspinus*, suggesting that these two genera originated in the middle to high southern latitudes with subsequent dispersal to more northern latitudes. Such an origination and dispersal pattern was originally described by Zinsmeister and Feldmann (1984) and was expanded upon by Schweitzer (2001). Currently, at least five genera with this origination and dispersal pattern are known, including *Palaeopinnixa* Via, 1966; *Chasmocarcinus* Rathbun, 1898; *Calappa* Weber, 1795; *Trichopeltarion*; and *Asthenognathus* (Feldmann and Zinsmeister, 1984; Feldmann and Wilson, 1988; Schweitzer and Feldmann, 2001a; Schweitzer, 2001). The pattern

originally described by Zinsmeister and Feldmann (1984) continues to be supported by fossil evidence.

Decapods collected from late Miocene rocks of Península Valdés are currently under study by some of us (SC, RF, AP, and CS), and these rocks share few genera with either the Centinela or Foyel formations. One or both of the two most commonly encountered genera in southern South America, *Chaceon* and *Proterocarcinus*, are found in each of the units mentioned here and are also abundant in all units in which they occur, so apparently they were highly successful ecological generalists during the Oligocene–late Miocene.

*Proterocarcinus* is the only genus common to both Maastrichtian–Danian rocks (Feldmann et al., 1995) and late Oligocene–early Miocene rocks of southern Argentina. The composition of the decapod fauna in southern Argentina therefore diverged greatly during the Paleocene–Oligocene interval, probably due to changes in sea level and in circulation patterns due to continued continental breakup. Clearly, the paleoenvironmental situation in southern South America was conducive to the evolution of diverse and specialized decapod faunas. Resolution of these issues is ongoing (SC, RF, AP, and CS).

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#### LITERATURE CITED

- AGUIRRE-URRETA, M. B. 1987. La familia Geryonidae (Crustacea, Brachyura) en el terciario de Patagonia y Tierra del Fuego, Argentina. IV Congreso Latinoamericano de Paleontología, Bolivia, 1:459–484.
- AGUIRRE-URRETA, M. B., S. MARESSI, AND S. SANTILLANA. 1995. A new Eocene crab (Crustacea, Decapoda) from Seymour Island, Antarctica. *Antarctic Science*, 7(3):277–281.
- ALCOCK, A. 1898. Materials for a Carcinological Fauna of India. No. 3. The Brachyura Cyclometopa. Part I. The Family Xanthidae. *Journal of the Asiatic Society of Bengal*, 67(pt. 2, no. 1):67–233.
- . 1900. Material for a carcinological fauna of India, No. 6. The Brachyura Catametopa or Grapsoidea. *Journal of the Asiatic Society of Bengal*, 69(11:3):279–486.
- ALCOCK, A., AND A. R. S. ANDERSON. 1899. Natural history notes from H. M. Royal Indian marine survey ship “Investigator,” Commander T. H. Heming, R.N. commanding, Series III, No. 2. An account of the deep-sea Crustacea dredged during the surveying season of 1897–1898. *Annals and Magazine of Natural History*, 7(3):1–27, 278–292.
- ANDERSON, A. R. S. 1896. Natural History notes from the R. I. M. survey steamer “Investigator,” Commander C. F. Oldham, R. N. commanding, Series II, no. 21. An account of the deep sea Crustacea collected during the season 1894–1895. *Journal of the Asiatic Society of Bengal*, 65(2):88–106.
- BAHAMONDE, N. N., AND D. FRASINETTI. 1980. *Lebucarcinus* n. gen. del Mioceno de Chile (Crustacea, Decapoda, Brachyura). *Boletín de Museo Nacional de Historia Natural, Chile (Santiago)*, 37:275–279.
- BALSS, H. 1932. Über einige systematisch interessante Xanthidae (Crustacea Decapoda Brachyura) der Harmsschen Reisen nach dem Sundaarchipel. *Zeitschrift für Wissenschaftliche Zoologie*, 142:510–519, figs. 1–4.
- BARREDA, V., V. GARCÍA, M. E. QUATTROCCHIO, AND W. VOLKHEIMER. 2003. Edad y paleoambiente de la Formación Río Foyel, cuenca Ñirihuau, provincia de Río Negro, Argentina. 12 Simposio Argentino de Paleobotánica y Palinología, Resúmenes: 8–9.
- BERTELS, A. 1980. Foraminíferos (Protozoa) y ostrácodos (Arthropoda) de las “Lutitas de Río Foyel” (Oligoceno) de la cuenca de Ñirihuau, provincia de Río Negro, República Argentina. *Ameghiniana*, 17:49–52.
- . 1993. Foraminíferos bentónicos (Protozoa) de las “Lutitas de Río Foyel” (Oligoceno medio bajo) provincia de Río Negro, República Argentina. *Revista Española de Micropaleontología*, 25:23–58.
- . 1994a. Los foraminíferos planctónicos (Protozoa) de las “Lutitas de Río Foyel” (Oligoceno medio bajo), cuenca de Ñirihuau–Ñorquinco–Cushamen, provincia de Río Negro, Argentina. *Ameghiniana*, 31:187–194.
- . 1994b. Foraminíferos (Protozoa) y paleoambientes de las “Lutitas de Río Foyel” (Oligoceno medio bajo), cuenca de Ñirihuau–Ñorquinco–Cushamen, provincia de Río Negro, República Argentina. *Revista Española de Micropaleontología*, 26:99–108.
- CASADIO, S., R. M. FELDMANN, AND K. A. FOLAND. 2000.  $^{40}\text{Ar}/^{39}\text{Ar}$  age and oxygen isotope temperature of the Centinela Formation, southwestern Argentina: An Eocene age for crustacean-rich “Patagonian” beds. *Journal of South American Geology*, 13:123–132.
- CASADIO, S., G. R. GUERSTEIN, S. MARESSI, S. SANTILLANA, R. FELDMANN, A. PARRAS, AND C. MONTALVO. 2000. Evidencias para una edad oligocena de la Formación Centinela, suroeste de Santa Cruz, Argentina. Resúmenes de la Reunión Anual de Comunicaciones de la APA, Ameghiniana, 37(4):71R.
- CAZAU, L. B. 1980. Cuenca de Ñirihuau–Ñorquinco–Cushamen. In J. C. M. Turner (Cordinador) *Geología Regional Argentina*, 2:1149–1172.
- CAZAU, L., D. MANCINI, J. CANGINI, AND L. SPALLETI. 1989. Cuenca de Ñirihuau. Pp. 299–318. In *Cuencas Sedimentarias Argentinas* (G. Chebli and L. Spalletti, eds.). Instituto Superior de Correlación Geológica, Serie de Correlación Geológica N° 6, 512 pp. Tucumán.
- CHIESA, J. O., AND H. H. CAMACHO. 2001. Invertebrados marinos eocenos de la parte inferior de la Formación Río Foyel, provincia



- de Río Negro, Argentina. *Revista Española de Paleontología*, 16: 299–316.
- CHIRINO-GÁLVEZ, L. 1993. Cenozoic crabs from Chile. Unpublished M. S. Thesis, Kent State University, Kent, Ohio.
- COLLINS, J. S. H., AND S. L. JAKOBSEN. 1994. A synopsis of the biostratigraphic distribution of the crab genera (Crustacea, Decapoda) of the Danian (Paleocene) of Denmark and Sweden. *Bulletin of the Mizunami Fossil Museum*, 21:35–46.
- COLLINS, J. S. H., AND H. W. RASMUSSEN. 1992. Upper Cretaceous–Lower Tertiary decapod crustaceans from West Greenland. *Grønlands Geologiske Undersøgelse Bulletin* 162, 46 p.
- CROSNIER, A. 1981. Découverte du genre *Trachycarcinus* dans l'Atlantique orientale. Description de *T. intesi* sp. nov. (Decapoda Brachyura). *Crustaceana*, 40(3):303–306.
- DALLA SALDA, L., AND J. FRANZESE. 1987. Las megafracturas del Macizo y la Cordillera Norpatagónica y la génesis de las cuencas volcanosedimentarias terciarias. *Revista Geológica de Chile*, 31:3–13.
- DANA, J. D. 1851. On the classification of the Caneroidea. *Silliman's American Journal of Science and Arts, Series 2*, 12:121–131.
- . 1852. *Macroura. Conspectus Crustaceorum and Conspectus of the Crustacea if the Exploring Expedition under Capt. C. Wilkes, U. S. N. Proceedings of the Academy of Natural Sciences of Philadelphia*, 6:10–28.
- . 1853. On the Classification and Geographical Distribution of Crustacea from the Report on Crustacea of the United States Exploring Expedition, under Captain Charles Wilkes, U.S.N., during the years 1838–1842. C. Sherman, Philadelphia, p. 1395–1592, 1 map.
- DAVIE, P. J. F. 2002. Crustacea:Malacostraca: Eucarida (Part 2): Decapoda–Anomura, Brachyura. Pp. xiv+641 p., in *Zoological Catalogue of Australia*, vol. 19.3B (A. Wells and W. W. K. Houston, eds.). CSIRO Publishing, Melbourne, Australia.
- DELL, R. K. 1968. A new crab of the genus *Trichopeltarion* from Australia. *Australian Zoologist*, 14(3):275–276.
- . 1969. A new Pliocene fossil crab of the genus (*Trichopeltarion*) from New Zealand. *Records of the Canterbury Museum*, 8(4):366–371.
- DIEZ, O. M., AND M. A. ZUBIA. 1981. Sinopsis estratigráfica de la región de "El Bolsón", provincia de Río Negro. *Asociación Geológica Argentina, Revista* 36:19–28.
- DOFLEIN, F. 1903. Die Augen der Tiefseekrabben. *Biologisches Centralblatt*, 23(16, 17):570–593.
- FABRICIUS, J. C. 1775. *Systema entomologiae, sistens, insectorum classes, ordines, genera, species, adiectis synonymis, locis, descriptionibus, observationibus*. Flensburgi & Lipsiae.
- FAXON, W. 1893. Preliminary descriptions of new species of Crustacea: Reports on the dredging operations off the west coast of Central America to the Galapagos, to the west coast of Mexico, and in the Gulf of California, in charge of Alexander Agassiz, carried out by the U. S. Fish Commission Steamer "Albatross," during 1891, Lieutenant Commander Z. L. Tanner, U. S. N., Commanding. IV. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 24(7):149–220.
- FELDMANN, R. M., AND M. T. WILSON. 1988. Eocene decapod crustaceans from Antarctica. Pp. 465–488, in *Geology and Paleontology of Seymour Island, Antarctic Peninsula* (R. M. Feldmann and M. O. Woodburne, eds.). Geological Society of America, Memoir 169.
- FELDMANN, R. M., AND W. J. ZINSMEISTER. 1984. New fossil crabs (Decapoda: Brachyura) from the La Meseta Formation (Eocene) of Antarctica: paleogeographic and biogeographic implications. *Journal of Paleontology*, 58:1046–1061.
- FELDMANN, R. M., S. CASADIO, L. CHIRINO-GÁLVEZ, AND M. AGUIRRE-URRETA. 1995. Fossil decapod crustaceans from the Jaguel and Roca Formations (Maastrichtian–Danian) of the Neuquén Basin, Argentina. *The Paleontological Society Memoir* 43 (Supplement to *Journal of Paleontology* 69), 22 p.
- FELDMANN, R. M., M. AGUIRRE-URRETA, L. CHIRINO-GÁLVEZ, AND S. CASADIO. 1997. Paleobiogeography of Cretaceous and Tertiary decapod crustaceans from southern South America: the link with Antarctica. Pp. 1007–1016, in *The Antarctic Region: Geological Evolution and Processes* (C. A. Ricci, ed.). Terra Antarctica Publication, Siena.
- FERUGLIO, E. 1949. Descripción Geológica de la Patagonia II: 1–349.
- FRANCHI, M. R., F. E. NULLO, E. G. SEPÚLVEDA, AND M. A. ULIANA. 1984. Las sedimentitas terciarias. 9 Congreso Geológico Argentino, *Relatorio* 1(9):215–266.
- GARASSINO, A., AND A. DE ANGELI. 2003. *Munida casadioi* (Schweitzer & Feldmann, 2000) from the Eocene of the Bariloche area, Patagonia (Argentina). *Contributions to Zoology*, 72:133–134.
- GLAESSNER, M. F. 1933. New Tertiary crabs in the collection of the British Museum. *Annals and Magazine of Natural History, series* 10(12):1–28, pls. 1–6.
- . 1960. The fossil decapod Crustacea of New Zealand and the evolution of the order Decapoda. *New Zealand Geological Survey Palaeontological Bulletin*, 31:1–79.
- . 1969. Decapoda. Pp. R400–R566, R626–R628, in *Treatise on Invertebrate Paleontology, Part R, Arthropoda 4* (R. C. Moore, ed.). Geological Society of America and University of Kansas Press, Lawrence, Kansas.
- GONZÁLEZ BONORINO, F. 1944. Descripción geológica y petrográfica de la Hoja 41b Río Foyel (ETR. Río Negro). Dirección Minas, Geología, Hidrogeología, Boletín, 56:1–124.
- GONZALEZ BONORINO, F., AND G. GONZALEZ BONORINO. 1978. Geología de la región de San Carlos de Bariloche: un estudio de las formaciones terciarias del Grupo Nahuel Huapi. *Asociación Geológica Argentina, Revista*, 33:175–210.
- GRIFFIN, M., L. M. PÉREZ, AND M. MURAVCHIK. 2002. Moluscos terciarios del Cerro Plataforma, en el noroeste de Chubut. 8 Congreso Argentino de Paleontología y Bioestratigrafía, *Resúmenes*: 101.
- GUERSTEIN, G. R., M. V. GULER, AND S. CASADIO. In press. Palynostratigraphy and paleoenvironments of the Oligocene/Miocene boundary from the Centinela Formation, southwestern Argentina. In *The Palynology and Micropaleontology of Boundaries* (A. B. Beaudoin and M. J. Head, eds.). Geological Society Special Publication.
- GUINOT, D. 1977. Propositions pour une nouvelle classification des Crustacés, Décapodes, Brachyours. *Compte Rendu Académie des Sciences de Paris, Serie D*, 285:1049–1052.
- . 1986. Une nouvelle espèce du genre *Trachycarcinus*, *T. crosnieri* sp. nov., de Madagascar (Crustacea Decapoda Brachyura). *Bulletin du Museum national d'Histoire naturelle, Paris, Série 4*, 1985(1986) A. (4):805–817.
- . 1989. Les genres *Trachycarcinus* Faxon et *Trichopeltarion* A. Milne Edwards (Crustacea, Brachyura: Atelecyclidae). In *Résultats des Campagnes MUSORSTOM, Vol. 5* (J. Forest, ed.). Mémoires du Muséum national d'Histoire naturelle (A), 144:347–385.
- GUINOT, D., AND T. SAKAI. 1970. Un nouveau *Trachycarcinus*, *T. elegans* sp. nov. (Crustacea Decapoda Brachyura). *Bulletin du Muséum national d'Histoire naturelle, Paris, Série 2*, 42(1): 201–205.
- DE HAAN, W. 1833–1850. Crustacea. Pp. 1–243, pls. A–J, L–Q, 1–55, in P. F. von Siebold, *Fauna Japonica sive Descriptio Animalium, quae in itinere per Japoniam, Jussu et Auspiciis Superiorum, qui Summum in India Batava Imperium Tenent, Suscepit, Annis 1823–1830 Collegit, Notis, Observationibus et Adumbrationibus Illustravit*. Lugduni-Batavorum, Leiden.
- IMAIZUMI, R. 1951. *Trachycarcinus luzioi* n. sp. from Yamagata Prefecture. *Short Papers, Tohoku University Institute of Geology and Paleontology*, 3:33–40.
- INTERNATIONAL CODE OF ZOOLOGICAL NOMENCLATURE. 1999. Fourth Edition. International Trust for Zoological Nomenclature, London, England.
- JAKOBSEN, S. L., AND J. S. H. COLLINS. 1997. New middle Danian species of anomuran and brachyuran crabs from Fakse, Denmark. *Bulletin of the Geological Society of Denmark*, 44:89–100.

- KARASAWA, H. 1990. Decapod crustaceans from the Miocene Mizunami Group, Central Japan. Part 2. Section Oxyryncha, Cancridea, and Brachyryncha. *Bulletin of the Mizunami Fossil Museum*, 17:1–33, 8 pls.
- . 1993. Cenozoic decapod crustaceans from Southwest Japan. *Bulletin of the Mizunami Fossil Museum*, 20:1–92, 24 pls.
- KARASAWA, H., AND H. KATO. 2003a. The family Goneplacidae MacLeay, 1838 (Crustacea: Decapoda: Brachyura): systematics, phylogeny, and fossil records. *Paleontological Research*, 129–151.
- . 2003b. Phylogeny, systematics and fossil record of the Goneplacidae MacLeay (Crustacea, Decapoda, Brachyura): revisit. *Contributions to Zoology*, 72:147–152.
- KATO, H. 1996. Miocene decapod Crustacea from the Chichibu Basin, Central Japan. *Transactions and Proceedings of the Paleontological Society of Japan, New Series*, 183:500–521.
- . 2001. Fossil decapod Crustacea from the Miocene Tomioka Group, Gunma Prefecture, Japan. *Bulletin of the Gunma Museum of Natural History*, 5:9–18 [in Japanese].
- LATREILLE, P. A. 1802–1803. *Histoire naturelle, générale et particulière, des crustacés et des insectes*. Volume 3. F. Dufart, Paris, France, 467 p.
- . 1831. *Cours d'Entomologie, ou de l'histoire naturelle des Crustacés, des Arachnides, des Myriapodes, et des Insectes*, etc. Annals I. Atlas. Roret, Paris.
- LEACH, W. E. 1814. *Crustaceology*. The Edinburgh Encyclopedia, 7: 383–437.
- . 1815. The zoological miscellany: being descriptions of new, or interesting animals, 2. London, p. 1–154, pls. 61–120.
- . 1820. *Galatéadées*. *Dictionnaire des Sciences Naturelles*, 18: 49–86. Paris.
- MACLEAY, W. S. 1838. On the Brachyurous Decapod Crustacea brought from the Cape by Dr. Smith. Pp. 53–71, pls. 1–2, in *Illustrations of the Annulosa of South Africa; being a portion of the objects of Natural History chiefly collected during an expedition into the interior of South Africa, under the direction of Dr. Andrew Smith, in the years 1834, 1835, and 1836; fitted out by "The Cape of Good Hope Association for Exploring Central Africa."* London.
- DE MAN, J. G. 1879. On some new or imperfectly known podophthalmous Crustacea of the Leiden Museum. Note XIX. Notes from the London Museum, 1:53–73.
- MANNING, R. B., AND D. L. FELDER. 1991. Revision of the American Callinassidae (Crustacea: Decapoda: Thalassinidea). *Proceedings of the Biological Society of Washington*, 104:764–792.
- . 1981. West African brachyuran crabs (Crustacea: Decapoda). *Smithsonian Contributions to Zoology*, 306:1–379.
- . 1989. Two new genera and nine new species of geryonid crabs (Crustacea, Decapoda, Geryonidae). *Proceedings of the Biological Society of Washington*, 102:50–77.
- MARTINS-NETO, R. G. 2001. Review of some Crustacea (Isopoda and Decapoda) from Brazilian deposits (Paleozoic, Mesozoic, and Cenozoic) with descriptions of new taxa. *Acta Geologica Leopoldensia*, XXIV(52/53):237–254.
- MIERS, E. J. 1886. Report on the Brachyura collected by H. M. S. Challenger during the years 1873–1876. Report on the Scientific Results of the Voyage of H. M. S. Challenger during the years 1873–1876. *Zoology*, 17:362 p., pls. 1–29.
- MILNE EDWARDS, A. 1862–1865. *Monographie des crustacés de la famille cancériens*. *Annals des Sciences Naturelles, Zoologie, Serie 4*, 18(1862):31–85; 20(1863):273–324; *Serie 5*, 1(1864):31–88; 3(1865):297–351.
- . 1880. Reports on the results of dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico and the Caribbean Sea, 1877, '78, '79, by the United States Coast Survey Steamer "Blake". . . VIII. Études préliminaires sur les Crustacés. *Bulletin of the Museum of Comparative Zoology at Harvard College*, 8:1–68.
- MONOD, TH. 1933. *Brachyura maroccana*, I. Pinnotheridae, avec description d'*Asthenognathus atlanticus* nov. sp. *Bulletin de la Société des Sciences Naturels du Maroc*, XII, no. 4–6, 1932[1933]:142–155, 9 figs.
- . 1956. Hippidea et Brachyura ouest-africains. *Mémoires de l'Institut Français d'Afrique Noir*, 45:1–674.
- MÜLLER, P., AND J. S. H. COLLINS. 1991. Late Eocene coral-associated decapods (Crustacea) from Hungary. *Contributions to Tertiary and Quaternary Geology*, 28:47–92.
- NAGAO, T. 1932. Two Tertiary and one Cretaceous Crustacea from Japan. *Journal of the Faculty of Science, Hokkaido Imperial University, series 4, Geology and Mineralogy*, 2:15–22, pl. 4.
- . 1941. On some fossil Crustacea from Japan. *Journal of the Faculty of Science, Hokkaido Imperial University, series 4*, 6:85–100.
- ORTMANN, A. E. 1893. Die Dekapoden-Krebse des Strassburger Museums. 7. Theil. Abtheilung: Brachyura (Brachyura genuina Boas) 2. Unterabtheilung: Cancroidea, 2. Section Cancrinea, 1. Gruppe: Cyclometopa. *Zoologischen Jahrbücher, Abtheilung für Systematik, Geographie und Biologie der Thiere*, 7:411–495.
- . 1894. Die Decapoden-Krebse des Strassburger Museums. *Zoologische Jahrbücher, Abteilung Systematik*, VIII:683–772.
- D'ORBIGNY, A. 1842. *Voyage dans l'Amérique méridionale, 1826–1833 (III). Géologie et Paléontologie*. Paris, France.
- PHILIPPI, R. A. 1887. Los fósiles terciarios i cuaternarios de Chile. Brockhaus, Leipzig (German version) and Santiago de Chile (Spanish version).
- POHLE, G., AND F. MARQUES. 1998. Phylogeny of the Pinnotheridae: larval and adult evidence, with emphasis on the evolution of gills. *Invertebrate Reproduction and Development*, 33:229–239.
- PORTER, C. 1910. Sobre la Antropología, Fauna y Floras Chilenas: Brevísimas consideraciones, Apéndice. Pp. 523–537, in *Chile en 1910* (E. Pourier, ed.). Imprenta and Litografía Barcelona, Santiago de Chile.
- PÖTHE DE BALDIS, E. D. 1984. Microfloras cenozoicas. 9 Congreso Geológico Argentino. *Relatorio II(4)*:393–411.
- RAFINESQUE, C. S. 1815. *Analyse de la nature, ou tableau de l'Univers et des corps organisés*. L'Imprimerie de Jean Barravecchia, Palermo, Italy.
- RAMOS, V. 1982. Las ingresiones pacíficas del Terciario en el norte de la Patagonia (Argentina). 3 Congreso Geológico Chileno, A263–A288.
- . 1999. Los depósitos sinorogénicos terciarios de la Región Andina. In *Geología Argentina* (R. Caminos, ed.). Instituto de Geología y Recursos Minerales. *Anales* 29(22):651–682.
- RATHBUN, M. J. 1898. The Brachyura of the Biological Expedition to the Florida Keys and the Bahamas in 1893. *Bulletin from the Laboratories of Natural History of the State University of Iowa*, 4(3):250–294, pls. 1–9.
- . 1902. Descriptions of new decapod crustaceans from the west coast of North America. *Proceedings of the United States National Museum*, 24(1272):885–905.
- . 1909. New crabs from the Gulf of Siam. *Proceedings of the Biological Society of Washington*, 22:107–114.
- . 1932. Preliminary descriptions of new species of Japanese crabs. *Proceedings of the Biological Society of Washington*, 45: 29–38.
- . 1945. Decapod Crustacea. Pp. 373–383, pl. 53–62, in *Geology of Lau, Fiji* (H. S. Ladd and J. E. Hoffmeister, eds.). Bernice P. Bishop Museum, Bulletin 181. Honolulu, Hawaii.
- RICHARDSON, L. R., AND R. K. DELL. 1964. A new crab of the genus *Trichopeltarion* from New Zealand. *Transactions of the Royal Society of New Zealand. Zoology*, 4(7):145–151.
- DE SAINT LAURENT, M. 1973. Sur la systématique et la phylogénie des Thalassinidea: définition des familles des Callinassidae et des Upogebiidae et de cinq genres nouveaux (Crustacea Decapoda). *Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, Paris, séries D*. 277:513–516.
- SAKAI, T. 1976. *Crustacea of Japan and the Adjacent Seas*. Kodansha Ltd., Tokyo, Japan.



- SALVA, E. W., AND R. M. FELDMANN. 2001. Reevaluation of the family Atelecyclidae (Decapoda: Brachyura). *Kirtlandia* (Cleveland), 52: 9–62.
- SAMOUËLLE, G. 1819. *The Entomologist's Useful Compendium, or An Introduction to the Knowledge of British Insects*. London.
- SCHWEITZER, C. E. 2000. Tertiary Xanthoidea (Crustacea: Decapoda: Brachyura) from the West Coast of North America. *Journal of Crustacean Biology*, 20:715–742.
- . 2001. Paleobiogeography of Cretaceous and Tertiary decapod crustaceans of the North Pacific Ocean. *Journal of Paleontology*, 75:808–826.
- SCHWEITZER, C. E., AND R. M. FELDMANN. 1999. Fossil decapod crustaceans of the late Oligocene to early Miocene Pysht Formation and the late Eocene Quimper Sandstone, Olympic Peninsula, Washington. *Annals of Carnegie Museum*, 68:215–273.
- . 2000a. First notice of the Chirostylidae (Decapoda) in the fossil record and new Tertiary Galatheididae (Decapoda) from the Americas. *Bulletin of the Mizunami Fossil Museum*, 27:147–165.
- . 2000b. New fossil portunids from Washington, USA, and Argentina, and a re-evaluation of generic and family relationships within the Portunoidea Rafinesque, 1815 (Decapoda: Brachyura). *Journal of Paleontology*, 74:636–653.
- . 2000c. Re-evaluation of the Cancridae Latreille, 1802 (Decapoda: Brachyura) including three new genera and three new species. *Contributions to Zoology*, 69:223–250.
- . 2001a. Differentiation of the fossil Hexapodidae Miers, 1886 (Decapoda: Brachyura) from similar forms. *Journal of Paleontology*, 75:330–345.
- . 2001b. New Cretaceous and Tertiary decapod crustaceans from western North America. *Bulletin of the Mizunami Fossil Museum*, 28:173–210.
- SCHWEITZER, C. E., AND E. W. SALVA. 2000. First recognition of the Cheiragonidae Ortmann (Decapoda: Brachyura) in the fossil record and comparison of the family to the Atelecyclidae Ortmann (Decapoda: Brachyura). *Journal of Crustacean Biology*, 20:285–298.
- SCHWEITZER, C. E., R. M. FELDMANN, A. B. TUCKER, AND R. E. BERGLUND. 2000. Eocene decapod crustaceans from Pulali Point, Washington. *Annals of Carnegie Museum*, 69:23–67.
- SCHWEITZER, C. E., R. M. FELDMANN, G. GONZÁLES-BARBA, AND F. J. VEGA. 2002. New crabs from the Eocene and Oligocene of Baja California Sur, Mexico, and an assessment of the evolutionary and paleobiogeographic implications of Mexican fossil decapods. *The Paleontological Society Memoir* 59 (Supplement to *Journal of Paleontology*, 76): 43 p.
- SCHWEITZER-HOPKINS, C. E., AND R. M. FELDMANN. 1997. Sexual dimorphism in fossil and extant species of *Callianopsis* de Saint Laurent. *Journal of Crustacean Biology*, 17:236–252.
- SEGERBERG, K. O. 1900. De anomura och brachyura dekapoderna inom Skandinavien Yngre krita. *Geologiska föringens i Stockholm förhandlingar* (Stockholm), 22:347–390.
- SERÈNE, R. 1964. Redescription du genre *Megaesthins* Rathbun et définition des Chasmocarcininae, nouvelle sous-famille des Goneplacidae (Decapoda Brachyura). *Crustaceana*, 7:175–187.
- SERÈNE, R., AND C. L. SOH. 1976. Brachyura collected during the Thai-Danish Expedition (1966). *Phuket Marine Biological Center Research Bulletin* No. 12:1–34.
- SPALLETTI, L. A. 1981. Facies sedimentarias de la Formación Ñirihuau en la región de San Carlos de Bariloche, provincia de Río Negro. *Asociación Geológica Argentina, Revista* 36:286–311.
- . 1983. Paleogeografía de la Formación Ñirihuau y sus equivalentes en la región occidental de Neuquén, Río Negro y Chubut. *Asociación Geológica Argentina, Revista* 38:454–468.
- SPALLETTI, L. A., AND L. H. DALLA SALDA. 1996. A pull apart volcanic related Tertiary Basin, an example from the Patagonian Andes. *Journal of South American Earth Sciences*, 9:197–206.
- SPALLETTI, L. A., AND S. D. MATHEOS. 1987. Composición de sedimentitas silicoclásticas terciarias de la cuenca de Ñirihuau (Patagonia occidental) y su significado tectónico. *Asociación Geológica Argentina, Revista* 42:322–337.
- ŠTEVČIČ, Z. 1991. Note on some rare and aberrant Australian crabs. Beagle, Records of the Northern Territory Museum of Arts and Sciences, 8:121–134.
- . 1996. Preliminary revision of the family Pinnotheridae. Abstract 87. VI Colloquium Crustacea Decapoda Mediterranea, Florence, Italy (unpublished).
- STIMPSON, W. 1858. *Crustacea Ocyropoidea: prodromus descriptionis animalium evertebratorum, quae in Expeditione ad Oceanum Pacificum Septentrionalem, a Republica Federata missa, Cadwaladaro Ringgold et Johanne Rodgers Ducibus, observavit et descripsit, Pars V. Proceedings of the Academy of Natural Sciences of Philadelphia*, 1858, 93–110.
- . 1871. Preliminary report on the Crustacea dredged in the Gulf Stream in the Straits of Florida, by L. F. Pourtales, Assist. U.S. Coast Survey. *Bulletin of the Museum of Comparative Zoology, Harvard*, 2:109–160.
- TAKEDA, M., Y. MIZUNO, AND M. TAMAOKA. 1986. Some fossil crustaceans from the Miocene Morozaki Group in the Chita Peninsula, central Japan. *Kaseki no tomo* (Publications of the Tokai Fossil Society Nagoya), 28:12–22.
- TESSIER, G., C. BESCHIN, A. BUSULINI, AND A. DE ANGELI. 1999. Nuovi brachiuri Eocenici nella cava "Main" di Arzignano (Vicenza-Italia settentrionale). *Lavori-Società Veneziana di Scienze Naturali*, 24: 93–105.
- TÜRKAY, M. 1983. *Georgeoplax*, new genus for *Litocheira glabra* Baker, 1906 (Crustacea: Decapoda: Brachyura). *Australian Museum Memoir*, 18:101–105.
- VEGA, F. J., T. COSMA, M. A. COUTIÑO, R. M. FELDMANN, T. G. NYBORG, C. E. SCHWEITZER, AND D. A. WAUGH. 2001. New middle Eocene decapods (Crustacea) from Chiapas, México. *Journal of Paleontology*, 75:929–946.
- VIA, L. 1966. *Pinnixa (Palaeopinnixa) mytilicola*, nuevo braquiuro fósil, en el mioceno marino del Vallés (Barcelona). *Acta Geologica Hispanica*, 1:1–4.
- WEBER, F. 1795. *Nomenclator entomologicus secundum Entomologiam Systematicum ill. Fabricii adjectis speciebus recens detectis et varietatibus*. Chilonii and Hamburgi.
- WHITE, A. 1846. Notes on four new genera of Crustacea. *Annals and Magazine of Natural History*, 18(118):176–178, pl. 2.
- WITHERS, T. H. 1924. Some decapod crustaceans (*Callianassa* and *Ranina*) from the Oligocene of Washington state, U.S.A. *Annals and Magazine of Natural History* (14), 9:121–127.
- ZINSMEISTER, W. J., AND R. M. FELDMANN. 1984. Cenozoic high latitude heterochrony of southern hemisphere marine faunas. *Science*, 224:281–283.